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Reproductive enhancement by helpers and an experimental inquiry into its mechanism in the bicolored wren

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Summary. As part of continuing studies of sociality in the wren genus *Campylorhynchus* we have been studying the bicolored wren – a facultatively cooperative breeder – for the past 6 years in the central Venezuelan savanna. Reproductive groups have ranged in size from 2 to 5. In one of our study populations, only about 15% of the groups contained helpers, and nearly all these contained only a single male helper (Fig. 2). In an adjacent population, the majority of groups contained helpers, and more than half of these contained several helpers of either sex. Territory size is, on average, much smaller in the latter population. In these populations, the presence of a single helper is associated with a three-fold increase in reproductive success (Table 1). Additional helpers are not associated with further reproductive enhancement. Enhancement is chiefly due to an increased proportion of nest starts that eventually produce independent juveniles. This reproductive enhancement is not merely an epiphenomenon resulting from the presence of helpers on territories which are superior for other reasons, such as greater resource availability or the quality of particular parents. It is also not a function of the mean or variance in nestling feeding rate. Predator exclusion experiments, in which certain nests were artificially protected from terrestrial predators, suggested that the mechanism of reproductive enhancement was heightened effectiveness of nest defense. Helpers are usually nondispersers from the parental territory, and have always been found to be close relatives of the nestlings that they assist in rearing.

Introduction

Two of the most informative approaches to the understanding of social evolution are between-habitat comparisons of single species and within-habit comparisons of closely-related species that differ in social structure (Altmann 1974). In either comparison, the number of affected variables is minimized in an effort to identify key causal factors. In our study of social behavior in the wren genus *Campylorhynchus,* we have taken advantage of both approaches. Aspects of the social behavior, ecology, and life history attributes of the cooperatively breeding Stripe-backed Wren (*C. nuchalis*) have been under investigation in the Venezuelan *llanos* since 1974 (Wiley and Wiley 1977; Rabenold and Christensen 1979; Rabenold 1984, 1985; Wiley and Rabenold 1984). For the past 6 years, we have similarly examined a sympatric population of the bicolored wren (*C. griseus*), in which a small proportion of breeding pairs are assisted by one, or very rarely two, adult helpers. During the past 2 years, we have also studied an adjacent population of *C. griseus* in which adult helpers were more numerous and the frequency of groups with helpers was significantly higher. Interspecific and interpopulation ecological and demographic differences will be analyzed with respect to their effects on social structure in subsequent papers (Austad and Rabenold, in preparation; Rabenold and Austad, in preparation).

In this paper, we describe variation in the composition and size of reproductive groups for both populations of *C. griseus.* We also report on the gender and reproductive effects of helpers at the nest (Skutch 1961 a), relatedness of helpers to the

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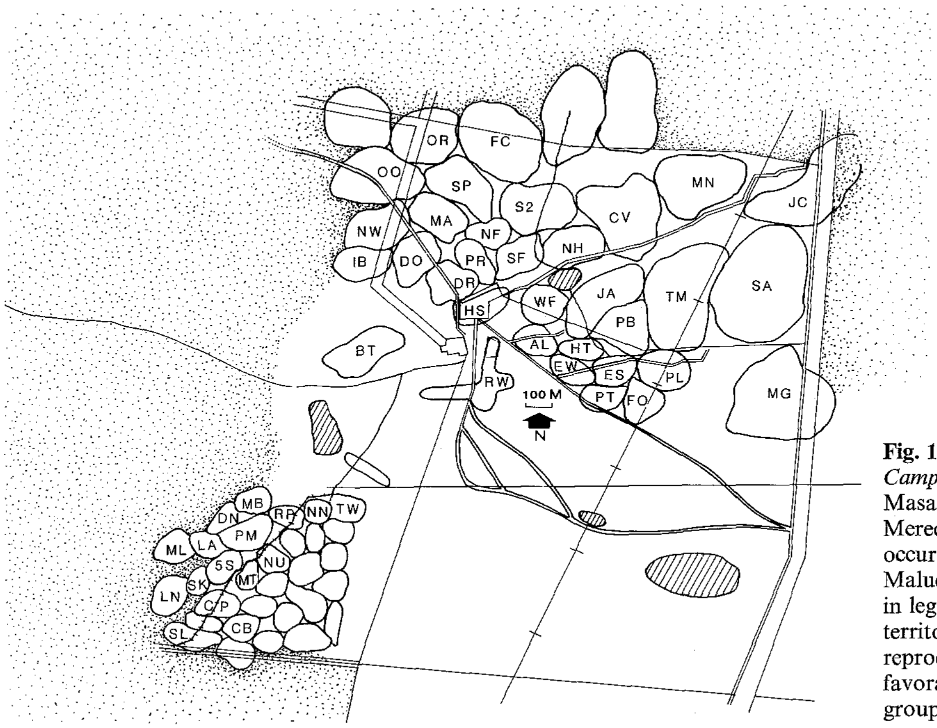

Fig. 1. Two populations of *Campylorhynchus griseus* under study at Masaguaral, Venezuela. The denser Merecure population in the southwest occurs in open palm savanna; the Maluenga population in the northeast is in legume-dominated woodland. Labelled territories were monitored for reproductive activities. Stippled area is favorable habitat and contains other groups

nestlings they help rear, and describe the experimental examination of a potential mechanism by which helpers increase group reproductive success. Avian helping behavior has been of continuing interest to evolutionary biologists because it offers an opportunity to critically examine Hamilton's (1964) inclusive fitness theory and Trivers' (1971) theory of reciprocal altruism in the evolution of aid-giving behavior across a range of environmental and demographic variables (Brown 1978, 1983; Emlen 1978; Emlen and Vehrencamp 1983; Vehrencamp 1979; Koenig and Pitelka 1981). Our data bear on these theories, and also provide a useful background for our forthcoming comparative analyses.

Methods

Study area. Our study sites are located on Hato Masaguaral, a working cattle ranch 45 km south of Calabozo (about 8 degrees N latitude) in the central Venezuelan savanna (*llanos*). Though temperature changes little throughout the year, the climate of the *llanos* is strongly seasonal, with 6 wet months (May-October), 4 dry months (December-March), and 2 transitional months (April and November) (Troth 1979). Yearly average rainfall is about 1,470 mm, though both amount and duration of precipitation are highly variable (SD = ±300 mm). Nearly all rainfall occurs in the wet season. Hato Masaguaral is a vegetational mosaic, ranging from open savanna to dense gallery forest (Troth 1979). It is variably flooded in the wet season, except for irregularly scattered sand-hills. During the dry season, standing water is practically nonexistent on our study sites.

The Maluenga population has been under study since 1977. It occupies varyingly dense shrub-woodland and palm savanna. Palms and leguminous trees dominate the shrub-woodland. From 1978 to 1981, we monitored 13 territories in the core of our current study area, which has now been expanded to include 30 contiguous territories with a total area of approximately 130 ha.

In January 1982, we began observations on the Merecure population, which occupies homogeneous palm savanna and is separated from the Maluenga area by 1–2 km of open treeless pasture (Fig. 1). Palms are nearly the only arboreal vegetation in this open savanna. Leguminous trees and shrub cover are much less abundant, palms are more dense, and wet season flooding is more extensive, than in the Maluenga area. In 1982, we closely monitored groups in 14 territories, and in 1983 we expanded our observations to 16 contiguous territories with a total area of about 20 ha.

Identification and sex determination. We color banded a total of 295 bicolored wrens during the study to date. The birds were inveigled into mistnets using playbacks of their duets. Juveniles were not banded until they had been fledged for at least 30 days. We measure wing chord and culmen length and record iris color on all birds, plus check all adults for the vascularized featherless brood patch characteristic of breeding females. We consider wrens to be adult at the beginning of the first breeding season after they have fledged, because both sexes have been known to successfully breed at this time. Adults can usually be sexed by chord length, although we have discovered during the past 2 years that there is a sexual dimorphism in vocalizations that is easily detectable to the unaided ear and has been 100% reliable (discussed further in Results). With respect to size, those wrens with chords shorter than 82 mm are invariably females, those with chords longer than 85 mm are (with one exception – see below) males. About 20% of adults have intermediate chord lengths. In the past these intermediately sized wrens could only be sexed when they achieved breeding status, although now they can be sexed by song. Provisional gender identification can later be verified as birds achieve breeding status, at which time only females develop brood patches and incubate eggs. The reliability of vocal gender identification has been checked with dozens of blind tests using known-sex adults, without a single mistake. In one case, vocalizations spurred us to reevaluate the gender identification of a pair we had previously only measured. We recaptured the birds and found, because the female now had a brood patch, that the pair contained an exceptionally large female and exceptionally small male, whose relative sizes had originally misled us.

In 1982 and 1983, when we accumulated the bulk of our data on nesting success, nestling feeding rates, and the reproductive contributions of individual helpers, 86% (137/159) of the adults in our study populations bore color bands. No more than a single bird in any territory lacked bands, making each individual within a territory identifiable.

Censusing and monitoring of reproduction. From 1978 to 1981, we determined the size and membership of all study groups twice per year – once in the dry season and once at the end of the wet season. Reproductive success of each group was summarized at the end of each wet season. In 1982 and 1983, our censuses were done once in the dry season, and twice in the wet season – at the beginning and the end. Reproductive success was recorded as it occurred. We used two census methods. Either we counted the birds out of the nest tree in the morning, then scoured the territory recording band combinations until the proper number of birds was accounted for, or (in the dry season) we simply used duet playbacks, which causes groups to assemble and perform shoulder-to-shoulder choruses. In assessing reproductive success, it is easy to distinguish unbanded juveniles from unbanded adults at the end of the wet season by a variety of characteristics (juveniles have darker irides, darker crowns, whiter breasts, shorter beaks, and inchoate song).

In 1982 and 1983, reproduction was monitored intensively in all groups. Territories were visited in a consistent sequence at maximum intervals of 5 days. Reproductive activity was documented by direct continuous observation of the principal female or the breeding nest, if its location were already known. Females or nests were observed for a minimum of 30 min. Nest observations in 1981 indicated that incubating females were never away from the nest for longer than 30 min, and usually for not longer than 15 min. During nestling feeding, periods of greater than 30 min without feeding are rare, and mainly confined to periods of heavy rainfall. It is possible that a small fraction of nesting attempts went undetected, especially if they failed in less than 5 days. However, because the observer visitation rate was equal across groups, undetected attempts should not be biased according to group size.

Rate of food delivery to nestlings was documented during 2-h or longer continuous nest observation periods. Generally nests are situated so that all individuals entering and leaving can be easily identified. Nests for which individual identification was only sporadically possible were watched to calculate gross feeding rates. However, those data were not used to assess the proportion of feeding by individual group members, because individuals tend to have stereotyped approaches to the nest entrance, and the sample of unidentified provisioners would be biased. We accumulated over 140 h of nestling feeding observations at a total of 22 different nests.

Predator exclusion experiment. Our principal clue that terrestrial predators might be a significant source of nest failure was that *C. griseus* consistently chose to nest in palms whose crowns could only be reached via the sheer palm trunk itself. Especially in the Maluenga area, where our experiments were performed, these palms are scarce. Most palms have various shrubs or strangler figs (*Ficus* spp.) associated with them, and this associated vegetation would allow easy indirect access to the palm crown from the ground. *C. griseus* never ($n = 77$) nested in palms whose associated vegetation did not leave at least 1 m of naked palm trunk above its highest growth.

With this observation in mind, in 1983 we chose 20 territories occupied by unaided pairs of wrens who had nested in palms the previous year. Ten of the territories were randomly selected to have antipredator devices installed on their nest trees, the other 10 served as controls. We chose to experiment with unaided pairs, because their normal level of nesting success (only 11% of pairs' nests produced fledglings in 1982) was sufficiently low that an increase resulting from the experimental treatment could potentially achieve statistical significance. Our antipredator devices consisted of a 1 m width of aluminum flashing tightly wrapped around the palm trunk above all associated vegetation. Once it was nailed in place, the flashing was thickly coated with chassis grease to mute the aluminum's reflective properties, maximize the efficacy of the device, and provide evidence in the form of tracks in the grease if any animal succeeded in surmounting it.

These antipredator devices would obviously only be effective against terrestrial predators. However, we had several reasons to suspect that terrestrial predators were a significant source of wren mortality in the nest. First, as noted above, the consistent physiognomy of nest trees suggested as much. Second, nearly all wrens observed mobbing other species in the breeding season were mobbing snakes ($n = 17$) and the single exception was the mobbing of a pygmy opossum (*Marmosa robinsoni*). Third, other Neotropical ornithologists have noted the prevalence of snake predation on small land birds (Snow 1962; Skutch 1976).

Antipredator devices were fitted as soon as the palm nest tree in a territory could be clearly identified, either because incubation had begun, or because the tree had become a focus of wren activity, suggesting that breeding was about to start. The territories used in our experiment were assigned to be controls or experimentals before the breeding season began. After incubation was detected, one territory was switched from experimental to control, and an adjacent territory was switched from control to experimental, because the initially experimental pair nested in a palm which grew obliquely to the ground at about 45 degrees, instead of vertically. We feared our antipredator device might be ineffective on such a tree. In presenting our results we only consider 9 experimental and 9 control groups. We do this because one control group nested in a legume instead of a palm, and one experimental group did not make a detectable nesting attempt while we were in the field (although that group did breed successfully later in the season). Reproduction was monitored in both experimental and control groups as in the rest of the study populations.

Results

Natural history

Bicolored wrens defend territories year-round, but reproduce only in the wet season, like most other insectivorous birds in the *llanos* (Thomas 1979). Territory boundaries are stable across time, even though there may be considerable turnover in ownership or change in group size. Advertising vocalizations are performed by all resident adults, either alone (solos), with another adult (duets), or as part of a larger group (choruses). Solos consist of 2 to 4 notes in a stereotyped melodic sequence often repeated several times, sometimes terminated by 3 to 6 harsh notes. Male and female solos are easily distinguishable by the unaided ear. Male solos consist entirely of short simple notes, whereas female solos invariably include at least one trill. Male-female duets are very common, consisting of simultaneous solos with the notes interposed. Male-male duets are uncommon, and are constituted of simultaneous solos with the notes superimposed. Female-female duets have never been observed.

Both sexes, including adult helpers when present, participate in territorial and nest defense, as well as in nest construction and maintenance, but only a single female breeds in any group. Only the breeding female incubates eggs and broods nestlings, but all adults feed nestlings and recent fledglings. Both incubation and the nestling period last about 17 days. Once fledged, juveniles are fed at a steadily decreasing rate for about 30 days, at which time we consider them "independent". Both sexes can, and often do, breed in the first wet season following their birth.

The ecology of bicolored wrens is dominated by the common palm, *Copernicia tectorum* (the wren's local common name is *cucarachero palmero,* or palm wren), which occurs wherever there is arboreal vegetation in the *llanos*. In the past two years, 87.5% ($n=88$) of breeding nests were built in palms. These covered grass nests are usually wedged among dead petioles just beneath the actively growing palm crown. Nest entrances are only large enough for one bird at a time to enter or leave. More rarely (9.1%), similar breeding nests are constructed within clumps of mistletoe in other tree species, and very rarely (3.4%) *C. griseus* appropriates stick nests built by thornbirds (*Phacellodomus rufifrons*). Even when not breeding, wrens nearly always sleep in dormitory nests (Skutch 1961b) which are indistinguishable from breeding nests and are also found in palms. During the breeding season all group members will sleep in the same tree, but they may sleep in several different trees during the dry season. The nests are cryptic both from the air and the ground. Bicolored wrens also spend the majority of their foraging time in palms.

Size and composition of reproductive groups

Reproductive groups ranged in size from 2 to 5 adults, though most consisted of unaided pairs. Group size was significantly larger in the Merecure than in the Maluenga area whether all years (Fig. 2), or only within-year variation, were considered (Mann Whitney U, $P<0.001$ for all comparisons).

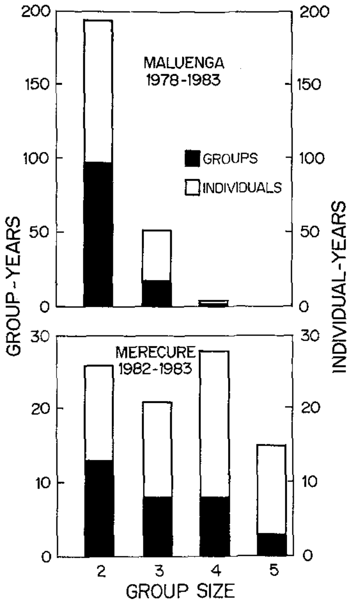

Fig. 2. Frequency distribution of reproductive group size in two populations of *C. griseus*. Number of group-years is shown by dark shading, number of individual-years by no shading. For Maluenga population, total group-years = 115, total individual-years = 249, mean group size = 2.17. For Merecure population, total group-years = 30, total individual-years = 90, mean group size = 3.00

In the Maluenga, a small fraction of breeding pairs, fluctuating irregularly between 6 and 22%, had helpers (usually only one) in each of the 6 years of our study. In 115 group-years, only one group ever contained as many as two adult helpers. Helpers were 7.6% of the adult population and all known-sex helpers ($n=12$) were males aged one or two.

In contrast, in the Merecure area, reproductive groups with helpers were in the majority (57%). Exactly one-third of the adult population ($n=56$) consisted of helpers, and one-third of those helpers were females. Age of helpers in this population is unknown except for one-year-olds, because of the brevity of the study to date. In 1983, 6 of 10 helpers, about whom we had information, were yearlings.

We estimated densities of the two populations by calculating the area of convex polygons circumscribing all the territories in our study populations and counting all resident adults within the polygon. In the Maluenga area, densities were 0.53 and 0.48 adults/ha in 1982 and 1983, respectively. The corresponding density estimates for the Merecure area were 2.33 and 2.40 adults/ha (see also Fig. 1). Adult densities were higher in the Merecure both because territories are, on average, much smaller and because group size is significantly larger. The Merecure area was also more productive of juvenile wrens (0.65 juveniles/ha/year versus 0.10 juveniles/ha/year in the Maluenga area) due to the same two factors (see below).

Reproductive effects of helpers

Reproductive success in all the following analyses is computed as number of juveniles surviving until 30 days past fledging – the time after which adults no longer feed them. Additionally, we only consider nonreproductive adults helpers. Young-of-the year have been observed to feed nestlings of later clutches, but they do so clumsily and infrequently, and have never assisted in the success of a second clutch.

Throughout our study, the presence of one or more helpers has been associated with a dramatic increase in group reproductive success. Pairs have produced an average of 0.57 juveniles/group-year ($n=97$ group-years), whereas groups with helpers have averaged 1.43 juveniles/group-year ($n=35$ group-years) ($P<0.001$, Mann-Whitney U, one-tail). The same trend was found across years and between study populations (Table 1). Reproductive enhancement was no greater, however, with several helpers (1.54 juveniles/group-year, $n=11$) than with just one (1.38 juveniles/group-year, $n=24$) ($P>0.95$, Mann-Whitney U, one-tail).

Table 1. Parameters of reproduction for 2 populations of *C. griseus* in 1982 and 1983

Study area	Helpers	Group-years	Nest starts	Juveniles produced	Percent nesting success	Juveniles per group-year
Maluenga	0	35	39	14	20.5	0.40
	1	10	14	14	42.9	1.40
Merecure	0	13	16	6	18.8	0.46
	1	7	9	8	44.4	1.14
	2	7	9	9	55.0	1.29
	3	3	4	4	50.0	1.33

Reproductive enhancement associated with the presence of helpers is necessary, but not sufficient, evidence that helpers are directly responsible for the enhancement. Helpers may be associated with groups which are reproductively superior for other reasons (Lack 1968). Ideally we would like to be able to partition the variation in group reproductive success into proportions resulting from variation in territory quality, parental quality, the presence of helpers, and stochastic processes. At present our data do not allow this level of refinement; however, the data do allow us the following conclusions. First, although territories of superior quality may more often contain helpers, there is reproductive enhancement when helpers are present over and above that due to territory quality alone. Our eight most productive territories in the Maluenga population contained helpers in some but not all years of the study. Reproductive success in those territories was significantly higher (1.58 juveniles/group-year, $n=12$) in those years when helpers were present than in years when they were absent (0.86 juveniles/group-year, $n=22$) ($P<0.025$, Mann-Whitney U, one-tail). Second, there is significant variation in territory quality. Unaided pairs on the superior territories mentioned above show significantly greater reproductive success than do unaided pairs in the rest of the population (0.86 vs 0.46 juveniles/group-year, $P<0.05$ Mann-Whitney U, one-tail). Third, parental experience appears thus far in the study to have little effect on group reproductive success. Considering unaided pairs only, yearling females produced an average of 0.25 juveniles ($n=8$) whereas older females produced 0.44 juveniles ($n=18$) ($P>0.2$, Mann-Whitney U, one-tail). Although this difference is statistically insignificant, there is a provocative trend and larger sample sizes may eventually reverse this conclusion. Male age (first year males average 0.60 and older males average 0.73 juveniles/year) and duration of the pair bond (first year pairs average 0.58 juveniles and pairs with one or more years together average 0.55 juveniles/year) do not increase reproductive success ($P>0.9$ in both cases, Mann-Whitney U, one-tail).

Detailed observations on reproductive attempts revealed that helper reproductive enhancement is largely due to an increase in the proportion of nesting attempts successful in fledging young (Table 1). There were only minor differences in the frequency of nesting attempts (1.15/year for pairs vs 1.33 for groups with helpers) or size of successful clutches (1.73 for pairs, 2.00 for groups with helpers) ($P>0.5$, Mann-Whitney U, one-tail, in both cases), but pairs produced independent young from only 20% of their nesting attempts, while groups with helpers succeeded in 47% of their nests.

The mechanism of reproductive enhancement

If the major effect of helping behavior is to increase the proportion of nesting attempts that are successful, there are two broad classes of mechanisms through which the effect might occur: (1) increased, or more reliable, feeding of nestlings, or (2) more efficient nest defense against predators and/or parasites.

Sufficiency of nestling feeding is always difficult to ascertain unless nestlings are repeatedly counted and weighed. Because bicolored wrens have closed nests we did not have direct access to nestlings, therefore had to rely on observation of rates at which food was delivered to the nest. Whether a given rate is sufficient depends upon the number and developmental stage of nestlings, as well as upon the size and quality of items fed. Gross feeding rates are highly variable (Fig. 3), and the variability is not an artifact of the length of the observations. In the data used for Fig. 3, more variability occurs in feeding by 4 adults, which were observed for 7 periods averaging 4.2 h than occurs in feeding by an unaided pair observed during 5 nest watches of 2 h each. Both of these groups has 3 nestlings during the final week before fledging.

Several lines of evidence suggest that feeding sufficiency is not implicated in reproductive enhancement. First, the tendency for nests of unaided pairs to fail more frequently than those of groups with helpers is more accentuated during incubation (40% vs 19% of nest starts fail) than during feeding and post-fledging dependency (40% vs 34%). If feeding assistance were the principal mechanism of helping, it would be expected that the largest difference in failure frequency would occur during feeding, particularly late in the feeding period when demands of nestlings would be greatest. Second, there is no statistically significant difference in mean feeding rates between pairs and larger groups ($P > 0.8$, Mann-Whitney U, two-tail) during the last week of the nestling phase, when food demand should be highest. Observed feeding rates were even slightly higher for pairs (11.4 feedings/h, SD = 2.5, 3 nests) than larger groups (9.9 feedings/h, SD = 4.3, 5 nests). In addition, feeding rates at nests which failed (9.1 feeding/h, 52 h of observations at 8 nests) were statistically indistinguishable from rates at successful nests (8.9 feedings/h, 104 h of observation at 11 nests) ($P > 0.95$, Mann-Whitney U). Finally, supposing that mean feeding rate is not the crucial variable, but that feeding constancy is important, note that the variance in feeding rate is also slightly, if insignificantly ($P > 0.5$, F-test), higher for groups with helpers.

If the quantity or reliability of nestling feeding is not the main source of reproductive enhancement, what about improved nest defense? During reproduction, these wrens will attack birds, snakes, or small mammals approaching the crown of the nest tree. An extra adult is not only an extra set of eyes, it also provides relief in feeding which might also allow the breeding pair to be more vigilant. Helpers *do* provide significant relief in the feeding duties of the principal pair, especially for the breeding female (Fig. 4). A helper can also aid in harassing an observed nest predator. Bicolored wrens have been seen to attack and draw blood from several species of climbing colubrid (*Chironius fuscus, Spilotes pullatus, Dryadophis* spp.) and boid (*Constrictor constrictor*) snakes (Austad, personal observation; Rabenold, personal observation) as well as pygmy opossums (Austad, personal observation).

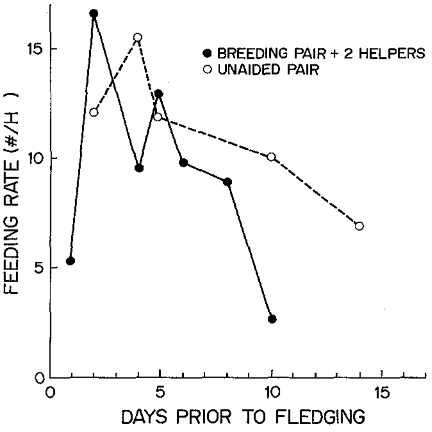

Fig. 3. Feeding rates of nestlings by an unaided pair and a pair with two male helpers. Data for the unaided pair were gathered during 2-hour observation periods. Data for the quartet were gathered during periods of variable length, ranging from 1.6 to 8.75 h (mean = 4.2 h)

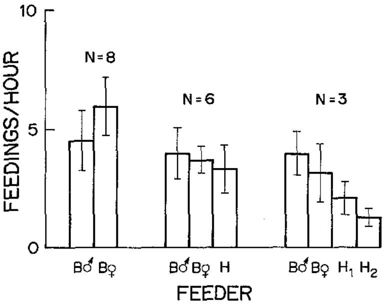

Fig. 4. Proportion of nestling feeding by individual group members. In all cases, the nests in question were observed for at least 8 h. Note that the presence of helpers (*H*) has little effect on feeding rate of the breeding male (*B*♂) whereas the breeding female (*B*♀) feeds much less often

Results of the predator exclusion experiments strongly suggest that predator defense is the key to reproductive enhancement. Experimental pairs produced an average of 1.67 juveniles per territory, while controls produced 0.44 juveniles per territory in their first nesting attempt. Two-thirds of the experimental nests and only one-third of control nests produced independent juveniles. Subsequent nesting attempts were not included in the analysis because they are not independent of the first attempts and statistical treatment would have been problematical. In any event, by late August, when we left the study site, the only additional fledglings were produced by an experimental group and when we returned in the dry season only an experimental group had produced more young. The magnitude of the effect produced by the antipredator experiments, both on productivity of juveniles and on nesting success, is similar to the observed differences for naturally-occurring pairs versus groups.

There are no obvious sources of bias in the direction favoring positive experimental results. In the previous year, the experimental territories produced fewer juveniles than did the control territories (0.11 vs 0.60). Thus if anything there is a counter-bias. In both experimental and control groups there were three new females whose ages were completely unknown; however, minimum ages of the other females (assuming they were in their first breeding season if banded as an adult) averaged 2.33 years in the experimental groups and 3.00 years in the controls. Again, if there were a bias it would favor negative results.

Needless to say, this experiment does not actually prove that the mechanism of helper reproductive enhancement is improved defense against terrestrial predators. Even groups with helpers normally have about a 50–60% nest failure rate, and it is conceivable that our predator shields affected a different subset of all possible predators than those against which helpers provide effective defense. For instance, groups with helpers may more effectively defend against diurnal birds of prey, which would not be deterred by our device. However, when our experimental evidence is combined with the additional knowledge that bicolored wrens place their nests in trees with difficult access for terrestrial predators, they are often seen mobbing climbing snakes, and that during breeding helpers always sleep in the nest tree whereas at other times they may sleep apart from the breeders, then the evidence is strongly suggestive.

Relatedness between helpers and nestlings

Geneological relationships between helpers and the nestlings they assisted in rearing are known for 17 birds in all – 11 in the Maluenga and 6 in the Merecure. Fourteen of these helpers (=82%) were rearing full sibs and the rest were rearing half-sibs or nephews. In every case but one the helper was a bird who had remained on his natal territory and assisted one, or both, parents during the following seasons. The single exception was a male who, together with his brother, annexed part of the parental territory. Therefore helpers have always been found to have a coefficient of relationship of at least 0.25 with the nestlings they help rear.

Discussion

The examination of avian social structure often proceeds by typological comparisons between species (but see Brown 1974; Stacey 1979; Craig 1980; Reyer 1980). However, as we have shown for the Bicolored Wren, even adjacent populations may differ significantly in social structure. Reproductive groups in the Merecure area not only contain, on average, more helpers, they contain helpers of both sexes, whereas only male helpers have been found in Maluenga. A first step in understanding observed patterns of avian social structure might be an understanding of how environmental and demographic variables affect whether male and female offspring choose to remain on their natal territory and assist in rearing close relatives, as opposed to dispersing to breed independently. At present, we will ignore the question of which sex should disperse (recent review by Greenwood 1980; Greenwood and Harvey 1982; Waser and Jones 1983), and concentrate on whether young of either sex should disperse.

Kin selection theory holds that helping behavior should evolve when helpers achieve greater inclusive fitness than nonhelpers (Hamilton 1964; West-Eberhard 1975). Inclusive fitness may be usefully partitioned into immediate and future direct fitness – reproductive success of the individual in question – and immediate and future indirect fitness – reproductive success of nondescendent kin, weighted by genetic relatedness (Brown 1980). Focusing for the moment only on immediate fitness components, the option of lone helping on one's natal territory appears always superior to dispersing in order to breed as part of an unaided pair, even assuming that a territory and mate can be found. A clear pattern in our data, in either population, is that a single helper increases reproductive success of the breeding group dramatically, yet additional helpers provide no detectable additional benefits. Unaided pairs produce about 0.4 (=0.2 offspring per capita), and groups with a single helper about 1.3, offspring per year (averages from Table 1). Thus a single helper is responsible for the production of 0.9 offspring/yr if helping to rear full-sibs, and the equivalent of 0.45 offspring/yr if rearing half-sibs. Even assuming no cost of dispersal, helping clearly appears to be the preferable option, unless nestlings are more distantly related than $r = 0.25$, as they never have been during our observations. This rather crude analysis accounts reasonably well for the social structure found in the Maluenga population. That is, when helpers occur, there is very rarely more than one in any territory, and they have always been related to the nestlings they rear at least as closely as half-siblings.

It may seem somewhat counterintuitive that helping is so advantageous and at the same time so rare. One could imagine a ratchet effect, whereby once a group produced a nondispersing offspring the group's productivity would jump, assuring a steady supply of future helpers. Two factors militate against this scenario. First, survivorship of independent juveniles during the first year is apparently low. Of the 57 we have banded over the years in the Maluenga, only 21 (=37%) have been seen as adults, despite the fact that we regularly use playbacks to thoroughly census the habitat surrounding our study area. No doubt some successful dispersers have gone undetected, but if first-year survivorship is remotely as bad as these data suggest then only about one pair in six would be expected to produce an adult offspring in any single year. Thus it would be very difficult for an unaided pair to get over the hump and produce a helper. Second, trios can be easily reduced back to pairs by mortality. Mean annual adult survivorship in this population has been 0.71 ($n = 163$) over the past 4 years. However, the mean disguises some extreme values. In our harshest year, annual survivorship was only 0.57, while in our mildest it was 0.90. Harsh years could decimate groups of three, and set the process of producing a helping offspring back to the beginning.

The breeding structure in the Merecure area is more problematic. There is no obvious short-term advantage to nondispersal for a wren maturing in a group already containing one or more helpers, except perhaps as a hedge against helper mortality or to allow older helpers to disperse, assuming older birds might experience a smaller cost of dispersal. Group-size-specific reproductive success is not significantly different in this population than in the Maluenga – several helpers do not increase group productivity any more than does one. Second or third helpers, then, are not increasing their immediate indirect fitness by nondispersal, and unless there are compensating long-term fitness effects, it would seem more beneficial to always disperse if one's natal territory already possessed a helper, even if dispersal costs were high. Yet breeding groups of 4 and 5 are common in the Merecure, and juveniles often fail to disperse although their natal territory already contains one or more helpers.

Perhaps long-term benefits are important (Selander 1964; Brown 1974; Ricklefs 1975; Koenig and Pitelka 1981; Wiley and Rabenold 1984). For instance, if dispersal is very risky, a young adult may stand a better chance of eventually achieving breeding status on its natal territory, than it would immediately in the surrounding population. Conditions especially favorable for this sort of long-term advantage would be low breeder, and high helper, survivorship. Preliminary indications are that this is not the case. Survivorship data from the Merecure population are still scant, but they suggest that breeder survivorship (=0.83, $n = 52$) is higher than that of helpers (=0.65, $n = 26$). The suggestion that helper survivorship may be relatively low reinforces the possibility that extra helpers could indeed remain as insurance against helper mortality during breeding. In addition, competition for any breeding vacancy would be keener in the denser Merecure population and because territories are smaller, wrens could audibly detect more vacancies without leaving their natal territory. While survivorship data for the two populations did not reveal significant differences in 1982 – a relatively mild year – there has been considerable survivorship variation over the years in the Maluenga population. Preliminary (6 mo) data by the end of 1983, suggests that in a harsh year survivorship will be considerably greater in the Merecure, than the Maluenga, population. Reduced incidence of breeder turnover could favor reduced dispersal in the Merecure. Models are now being developed to determine the minimum differences in life history parameters and sex-specific dispersal rules which could account for the observed divergence in social structure between these populations.

In conclusion, we have demonstrated that helpers in the bicolored wren do, in fact, augment reproductive success, that multiple helpers provide no more short-term reproductive enhancement than single helpers, and that the mechanism of the assistance is probably related to increased efficiency of nest defense against predators. These results are very similar to those from the study of the sympatric congeneric stripe-backed wren (*C.*

nuchalis) except that the threshold of effective group size is higher for this smaller wren (4 adults) and the increment in reproductive success attributable to helpers is somewhat greater (Rabenold 1984). The observed social structure of one of our study populations of Bicolored Wrens is seemingly understandable in terms of observed patterns of survivorship, and immediate gains in helper indirect fitness. In the more socially complex of our two populations, immediate gains in indirect fitness and preliminary survivorship patterns do not yield the same degree of understanding of the observed social structure. It is likely that a consideration of long-term costs and benefits of helping behavior will be vital to understanding this population.

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