Cooperation in breeding by nonreproductive wrens: kinship, reciprocity, and demography

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Summary. Stripe-backed wrens (*Campylorhynchus nuchalis*) often live as adults in large groups on permanent, communally defended territories. Nonbreeding adults cooperate in rearing the young of a single breeding pair; this aid substantially increases the reproductive success of the breeders. In a 6-year study in Venezuela of a completely colorbanded population of 25–30 groups, most adults participated in breeding only as helpers and priority to breeding status was strictly age-determined. Detailed behavioral observations at breeding nests with nestlings showed that, in a sample of 100, helpers nearly always contributed as much to the care of young as breeders. Further, aid-giving does not vary systematically with relatedness of young to helpers or with probability of future reciprocation by young. Young being raised are most often at least half siblings of helpers, but seldom return aid to adults that helped raise them. Even adopted helpers collaborate fully. Patterns of demography and dispersal show slow turnover of breeders, delayed reproduction, and a viscous population structure.

Application of Hamilton's condition for selection for aid-giving reveals that most individuals in this population can maximize inclusive fitness in the first 2 years by helping instead of breeding. Variation in helping effort and in age of first breeding is related to variation in natal group size and competition resulting from variable demographic neighborhoods in different years or in different parts of the population. Because reciprocation in the form of specific alliance formation among nonreproductives is uncommon, nonspecific reciprocity between cohorts and kin selection account well for the observed pattern of age-dependence in first breeding. Nondiscriminating helping in this population is associated with stable monogamous pair bonds, stable territory boundaries and group membership, strict seniority for breeding position, high viscosity and consistent effectiveness of aid. Under these circumstances, very simple behavioral rules amounting to nearly automatic helping seem sufficient to confer critical inclusive fitness gain on helpers.

Introduction

Individuals in a wide variety of vertebrate societies cooperate in accomplishing tasks too difficult for solitary animals or mated pairs. Such cooperation can directly and immediately benefit all participants, as in group hunting, but in many cases benefits are not apportioned evenly among all group members. When some collaborating animals receive little or no direct or immediate benefit from cooperative behavior, biologists have sought to identify mechanisms of indirect or delayed advantage to donors of aid (Hamilton 1964, 1972; Trivers 1971; Wilson 1975; Axelrod and Hamilton 1981; Brown 1983). Breeding in many societies of birds and mammals is practiced by only a few members at any one time, and when nonbreeding adults assist breeders in rearing young, the challenge to discover the adaptive basis of such aid-giving becomes acute (Williams 1966; Lack 1968; Alexander 1974; West-Eberhard 1975; Brown 1974, 1978, 1983; Emlen 1982; Ligon 1983). This paper describes helping behavior in groups of cooperatively breeding tropical wrens (*Campylorhynchus nuchalis*) and assesses the degree to which patterns of aid-giving can be explained by (1) kinship among group members, (2) reciprocation by recipients of aid, and (3) demographic conditions. I try to develop an understanding of how nondiscriminating aid-giving can be favored by certain pat-

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terns of dispersal and demography and by a stable social order.

Kinship

Cooperative breeding in birds commonly consists of aid given by helpers (auxiliaries likely to be non-reproductives) (Skutch 1961) to a pair of dominants (principals likely to be breeders) in a family group that maintains a communal territory. Helpers generally remain on their natal territories and are most often at least half-siblings to subsequent offspring that they attend (Rowley 1965; Woolfenden 1975; Maynard Smith and Ridpath 1972; and later papers reviewed by Brown 1978 and Emlen 1978). Aiding kin could, if effective, increase the inclusive fitness of helpers through kin (indirect) selection (Hamilton 1964, 1972; Brown 1974, 1980, 1983; West-Eberhard 1975; Wilson 1975; Maynard Smith 1976; Dawkins 1979; Vehrencamp 1979; Sherman 1980; Koenig and Pitelka 1981; Emlen and Vehrencamp 1983).

Kin selection requires that beneficial effects of an individual's actions be distributed so that genetically correlated recipients gain more than average recipients (Hamilton 1964; Michod 1982). Mechanisms by which this differential apportioning of benefit might be effected range from passive association to active discrimination of degrees of relatedness (Blaustein 1983; Holmes and Sherman 1983). Helping may only be advantageous above a threshold benefit/cost ratio that balances nondescendent kin production weighted by degree of relatedness against alternative offspring production (Hamilton 1964). Once this threshold is surpassed, aid could be distributed either among nondescendent kin proportional to relatedness or solely to the closest kin, depending on the need of each potential recipient (Dawkins 1979). In the absence of simultaneous alternative recipients, helpers might still adjust their efforts according to the degree of kinship with the available recipient. Recognition of exact genetic correlation between donor and recipient is not necessary for kin selection; helpers could use "rules of thumb" based on the social context to distribute aid nonrandomly to relatives.

Reciprocation

Reciprocation by recipients of aid can favor aid-giving even in the absence of close kinship (Trivers 1971; Packer 1977; Axelrod and Hamilton 1981; J.S. Brown et al. 1982; Ligon 1983). Nearly simultaneous reciprocity occurs in groups with more than one breeding individual and communal rear-

ing of young (Maynard Smith and Ridpath 1972; Mader 1975; Vehrencamp 1978; Dow 1978; Rowley 1978; Stacey 1979; Brown and Brown 1980; Craig 1980; Joste et al. 1982), but reciprocity that is more delayed is common in groups with a single breeding pair (Woolfenden and Fitzpatrick 1980; Ligon 1981; Wiley and Rabenold 1984). The probability of reciprocation from the viewpoint of a nonbreeding helper depends upon the probability that an opportunity to breed will arise in the group where aid was given while potential reciprocators are still members. This probability can be sex- or age-dependent (Woolfenden and Fitzpatrick 1978). Helpers might be expected to be more likely to aid in breeding when reciprocation is likely (Stallcup and Woolfenden 1978).

Demography

The cost of contributing to another individual's breeding efforts, especially when aid-givers defer their own reproduction, is generally calculated in terms of the helper's lost breeding potential (Brown 1975, 1983; West-Eberhard 1975). If breeding is an alternative to helping, then helping is advantageous only when lost breeding potential is balanced by either inclusive fitness gains through producing nondescendent kin (indirect fitness – Brown 1980) or later gains in reproductive potential through reciprocal cooperation (future direct fitness – Brown 1980; Wiley and Rabenold 1984). How much breeding potential is lost depends upon how frequent and how promising breeding opportunities are.

Demography of the population reflects the frequency of breeding opportunities and the competition for those opportunities. Opportunities for an individual to breed arise according to (1) the current level of resource monopolization by breeders (ecological saturation), (2) breeder mortality, and (3) competitor natality and survivorship (Brown 1969, 1974; Ricklefs 1975). Environmental limitation of breeding possibilities, such as scarcity of necessary food or cover, or predator pressure, can limit breeding to rare combinations of circumstances and create intense competition among would-be breeders. Inclusive fitness gains resulting from helping at a particular age depend upon the rate of decay of relatedness of a helper to nestlings that in turn is determined by breeder mortality and turnover. Probability of reciprocation depends in part on survivorship of juveniles to the age of reciprocation.

This paper tests the general hypothesis that aid-giving in cooperatively breeding societies is advan-

tageous to the donor. The three non-exclusive subsidiary hypotheses whose predictions will be explored are (1) that helping behavior is favored by inclusive fitness gains resulting from preferential aid-giving to nondescendent kin, (2) that helping behavior is favored by delayed reciprocation of aid-giving, and (3) that helping behavior is favored by demographic circumstances that make breeding opportunities scarce for young animals. Stripe-backed wrens (*Campylorhynchus nuchalis*) breed most successfully in large groups (Rabenold 1984) so that nonbreeders generally outnumber breeders in the population. Reproductive success in a large group can compensate for a delay in breeding of several years for these wrens (Wiley and Rabenold 1984). In order to test hypothesis (1) I will analyse the probability that helpers are associated with close kin and ask whether helping effort is adjusted to degree of kinship. Hypothesis (2) predicts that reciprocation will be common and effective in increasing the reproductive success of the donor; I will test this prediction and ask whether helping effort is adjusted to probability of reciprocation. To test hypothesis (3) I ask whether age-dependent patterns of mortality and fecundity are consistent with intense competition for breeding positions.

Methods

Study population. 26–30 groups of stripe-backed wrens (*Campylorhynchus nuchalis*) (Fig. 1) have been studied since July 1977 over approximately 120 ha at Hato Masaguaral, Estado Guárico in the savanna of central Venezuela (Wiley and Wiley 1977; Rabenold and Christensen 1979; Rabenold 1984). Territories are communally defended year-round by as many as 14 adult birds. Groups average 5 adults so that the main study population varies between 125–150 individuals. In addition, 5 outlying territories were studied in 1977–1979. The main study population occupies an open woodland habitat bounded on all sides except the north by grassy fields or marsh that are not utilized by wrens.

All members of the population were individually marked with colored plastic leg bands in 1977, and all subsequent young and immigrants have also been banded with unique color combinations. In 6 years, 365 wrens have been banded with individual color combinations in the study area. Wrens can be easily censused at dawn and dusk as they leave or enter their communal roosting nests. Censuses were recorded semiannually during and after the 6-month breeding season that lasts from April–September. Groups outside the study area were also censused at these times up to a distance of approximately 1 km, or from two to five territory widths, in all directions from the study population.

Behavioral interactions: sexing and aging. All members of stripe-backed wren groups participate in territory defense, nest building and defense, and all aid in feeding nestlings and fledglings. Stripe-backed wrens use two different kinds of nests for roosting and breeding: stick nests and grass nests. The former are large, conspicuous structures built by thornbirds (*Phacellodo-

Fig. 1. Stripe-backed wrens (*Campylorhynchus nuchalis*) duetting. This pair was a father and daughter. Drawing by Kathy Schuster

mus rufifrons) at the ends of branches of large trees. These structures are organized into several compartments and can be as tall as 2 m. During the breeding season, adults roost in one or two compartments separate from the nestling chamber. Wrens also construct nests of grasses and vines woven together usually in a clump of mistletoe in the branches of a tree.

All members of a stripe-backed wren group participate in vocal and tactile interactions. Wrens preen one another while the recipient adopts a stereotyped solicitation posture. All members of a group sing in duets that consist of rapidly alternating harsh notes by both partners while in close physical proximity (Wiley and Wiley 1977). One principal pair accounts for most of the duetting and preening in the group, especially in the vicinity of the nest; evidence is presented below that these are the only breeders.

Stripe-backed wrens are sexually monomorphic, but duetting combinations allow sexing of individuals. Matrices of duetting combinations show that nonbreeding helpers duet with one breeder but not the other and that helpers that duet with the same breeder do not duet with each other. Duetting partners are always of opposite sexes. Substantiation of this sexing technique comes from transfers between groups and ascension to breeding status. In 84 cases of transfers, birds fit into the duetting pattern of the new group in the same sex category as in the original group. Of 74 birds that have gained breeding status in 5 years, all have adopted the breeding role consistent with their previous duetting pairings.

Although juveniles have distinctive iris color and plumage, individuals can be aged beyond six months only by marking them and keeping individual records. By 1981 age and parentage were known for almost all helpers (95%), but many were marked in 1977 whose age could not be determined. These birds' histories could, however, be traced and their helping behavior and breeding histories recorded in minimum age categories (e.g. ≥ 2 year). Where this has been necessary, these birds are distinguished from known-age birds and corrections are used for the low bias in demographic calculations.

Group enhancement of reproductive success. I have shown in a separate paper (Rabenold 1984) that breeders aided by two or more helpers have much greater reproductive success than those with less help. Groups with 4 or more adults produce

more juveniles annually than smaller groups (2.4 vs 0.4), even on a per capita basis (0.47 vs 0.16). Large groups lose a much lower proportion of clutches of nestlings to predators (0.38) than small groups (0.87) and large groups are capable of successfully rearing multiple clutches in a season. Nestlings in large groups are not better fed, but feedings provided by helpers free the breeders from these duties. Helpers also help defend the nest against brood parasites and predators. Large groups probably suffer less predation of nestlings because of more effective nest defense. The relationship between group size and reproductive success is used in this paper to compare breeding and helping options open to helpers under various demographic circumstances.

Behavioral observations at nests. Breeding status of all groups was monitored at weekly intervals through the entire breeding season in 1978 (April–December) and 1979 (May–October) and through roughly half of the season in 1980 and 1981 (June–August). Observations of groups feeding nestlings were made between 0600 and 1200 hours with 10× binoculars. Records were kept of arrivals and departures of individuals; type, color, and size of food items brought; behavioral interaction among group members near the nest, especially duetting, allopreening and agonistic encounters; and interspecific interactions near the nest. Four groups were observed for at least 1 h each day through the entire 17 days of nestling feeding in order to establish the sampling effort necessary to characterize individual feeding effort. Six hours of observation on 6 days in the last half of the nestling phase were sufficient. Observations were balanced for time of day so that 2 periods fell between 0600–0800 hours, 2 between 0800–1000 hours, and 2 between 1000–1200 hours. No effect of time of day was found in either total feeding rate or relative individual contributions. Numbers of nestlings being fed were unknown because of the inaccessibility of the closed nests.

To characterize individual feeding effort in spite of varying numbers of both nestlings and other feeders, I use a relative measure of feeding effort:

$$P = f\left(\frac{N}{F}\right),$$

where f = number of feedings by an individual; F = number of feedings by all group members; N = number of group members.

P is the proportion of an equal share of feedings provided by an individual; when all group members contribute equally, $P = 1.0$ for all. P is a better measure of an individual's effort than f or f/F because stimulation from the begging of hungry nestlings will depend on both the number of nestlings and the number of other feeders. If F is proportional to the number of nestlings, weighting f by N/F should scale the absolute feeding performance of an individual to the stimulation received; this provides a relative index of motivation that can be used across groups.

Results

Behavioral dominance and parentage

Establishing relatedness of nonbreeders to the young they help to raise requires knowledge of parentage. The behavioral dominance expressed by one pair in a group over others in territory defense and duetting strongly suggests that these principals are in fact the only breeders. Both breeders some-

times intervene in duets between their mate and another bird. When one breeder is duetting with a helper the absent mate often abruptly approaches the duetters and finishes the duet in place of the helper. Physical supplantation by the arriving breeder sometimes occurs, but overt aggression is rare. Duetting breeders are never interrupted by helpers. Supplanted helpers sometimes solicit preening and the supplanting breeders then often oblige. The activity of the breeders in duetting, preening, and territory defense, and their primacy in these activities, make them easily distinguishable even in the nonbreeding season.

Although helpers often instigate boundary conflicts with neighboring groups, the breeding pair invariably responds very strongly to encroachment by other groups. The breeders display the strongest defense of territory especially when a challenge is experimentally provided in the center of the territory using recordings of neighboring wrens' vocalizations (Wiley and Wiley 1977; Rabenold and Christensen, unpublished data). When playbacks are used near the nest during mist-netting of the group, the breeders perform almost all duets in response, especially flying duets, while the helpers follow along and occasionally join in to form a chorus. When one of the breeders is caught, the mate remaining free will quickly begin duetting with an opposite-sex helper, usually the oldest.

Stripe-backed wrens normally mate for life. In 125 pair-years of observation, only 4 instances of mate-desertion have been observed; in all cases the female breeder left the group to breed elsewhere. When one mate dies, survivors of either sex remain and take another mate. In 6 cases, however, no male helper was present in the group to step into the breeding role, and the breeding female subsequently dispersed. In 2 cases of death of the breeding male, the only males left in the group were sons of the breeding female and she dispersed. Some evidence of incest avoidance therefore exists. Within the context of cooperative breeding, stripe-backed wrens are thoroughly monogamous.

Behavior of the breeders during egg-laying provides strong evidence that no others reproduce. Copulations are apparently confined to the chamber of the closed nest destined to receive the clutch of eggs. In more than 10,000 h of observation, not one copulation or preliminary behavior has been witnessed. It is highly unlikely that copulations occur outside the nest.

In the 2 weeks before egg-laying, the breeding male prepares either a chamber of a large nest or a small separate nest. In detailed observations of 5 different groups, behavior before and during egg-

laying followed the same pattern. The two breeders spent up to 5 min on several occasions just preceding egg-laying in the first hours after dawn together in the breeding nest. The female began laying eggs the following day in the same nest or chamber. During egg-laying and the first few days of incubation, the breeding male maintained a vigil at the entrance to the breeding chamber both when his mate was inside and when she was not. The male spent most of his time either at the nest entrance or nearby in the nest tree. This vigil probably served to defend both the site of copulation and the clutch. Shiny cowbirds (*Molothrus bonariensis*) were frequently chased away from the nest by the breeding male.

Because inferred parentage is critical to interpretations of cooperative breeding, I present below a detailed example that illustrates the close association of breeders at the nest before and during egg-laying. In June 1982, TM group comprised 5 wrens: the breeding male C who was at least 6 years old; the breeding female B, 4 years old from a neighboring group; a 2-year helper female W; and two yearling helpers, R male and G female who were half-siblings to W, offspring of B, and probably niece and nephew of C. We monitored the breeding activity of this group closely June 12–25, for a total of 25 h of direct observation, mostly in the early morning 0600–0900 hours at the group's nest. During the first week, activity at the nest consisted mostly of deliveries of nest-lining material by all members, especially the young helper R. Two chambers of the nest were in use, although only the breeders visited the lower chamber where eggs were later incubated by the breeding female. She visited the nest 74 times in 12.5 h (6 visits/h) and often lingered on the surface of the nest for several minutes, or entered the breeding chamber (29 times). The breeders were observed together inside the breeding chamber on 7 different occasions during this week, and these meetings lasted for from 10 s–5 min. The breeding female B duetted with the young helper male R at the nest nearly as often (14 times) as with her mate (15 times) and the breeding male C duetted with the young female G 7 times. B also allo-preened with R on several occasions. In spite of these friendly breeder-helper interactions, B attacked the older female helper W on three occasions and apparently kept W away from the nest. C occasionally displaced R and B sometimes did the same to G; overt aggression during this week was rare, and is usually rarer in other groups.

Egg laying began on June 22, and from June 21–25 the breeders maintained much closer contact. The breeders C and B duetted with each other more often than with the helpers (20 times vs 13) and C accompanied B to the nest more frequently (26 times in 12 h). The breeders entered the breeding chamber together another 8 times from June 21–23 but no others entered. During these rendezvous, C often quickly entered the chamber in front of B repeatedly as if to "entice" her inside. This behavior has been seen repeatedly involving breeders in other groups as well, and could be considered courtship. B continued to attack the older female helper W during these 5 days and C became less tolerant of duetting by R; C interrupted 3 of R's duets with B, supplanting the young male in the process. The helpers spent much less time at the nest than in the previous week. Breeding female B had an obviously swollen cloaca that was first noticed on June 22, the first day that she spent an extended time in the breeding chamber alone in the first hour after dawn (0613–0642). B spent 22–24 min in the nest soon after dawn on each of the next 3 days as well, presumably completing a four-egg clutch. On the morning of June 23, B emerged separately from the others at dawn having spent the night in the breeding chamber with the eggs. On June 25 B began regularly spending periods of 16–20 min incubating. On July 13, 18 days later, nestlings were being fed in the breeding chamber.

The breeding female is the only member of a group we have seen enter the breeding chamber until the eggs hatch, aside from her mate's brief rendezvous with her. Even when other members begin helping to feed nestlings, only the breeding female broods the young and sleeps with them overnight while the rest of the group sleeps in a separate compartment or nest. During the entire nesting cycle, the breeding male is the main defender of the nest against other species, including parasitic cowbirds (Rabenold 1984). Selander (1964) has found that *Campylorhynchus* groups do not normally contain more than a single female with a brood patch, but sometimes contain several males with at least partially developed testes. The female breeder in a group is identifiable by her vascularized brood patch in addition to the fact that no others incubate eggs or brood nestlings. In 130 group-years of observation, a second female with a brood patch has only been seen once, and in only one other group did a second female appear to do some brooding. The breeding male usually maintains close association with the breeding female. While helpers may be physiologically mature, our behavioral evidence suggests that only the breeding pair actually contributes to the clutch

that is later cared for by the entire group. Although it is difficult to exclude the possibility of occasional furtive copulations by the breeding female with helpers, no hint of courtship or copulation by helpers has been witnessed, and the exclusive occurrence of copulation in the nest controlled by the breeding male makes mating by male helpers improbable.

Opportunities to raise kin and reciprocate aid

Eggs are incubated by the breeding female for 18–21 days. The breeding female broods the chicks periodically during the day, for up to one hour at a time, and all night. As the nestlings grow, feeding rates increase, although there can be substantial hour-to-hour variability (Fig. 2). The breeding female reduces her brooding effort as the chicks mature, but still stays with them overnight.

All members of a group help in feeding nestlings; four examples are given in Fig. 3. In large groups, helpers provide as much as 80% of the food delivered to nestlings. Nestlings are not fed more in large groups; instead, adults compensate for the efforts of others and each contributes fewer deliveries than in small groups. Breeding males make considerably fewer deliveries in large groups than in small groups, but breeding females' feeding efforts are affected little by group size (Rabenold 1984).

Relatedness of helpers to the young they help raise is generally high in this wren population. For the 151 helper-years observed from 1978–1982 in which the helper was of known parentage, kinship between helpers and potential offspring in a group has been known in most cases ($n = 126$). For 110 first-year helpers, 73 (66.4%) were helping both parents in breeding attempts, although not all of these attempts were successful (Table 1). Most first-year helpers are in a position to contribute to the production of full siblings. Many fewer first-year helpers had the opportunity to help produce half siblings or quarter siblings ($n = 30$; 27.3%), or shared no parents with potential young (nonsiblings; $n = 7$; 6.4%) (Table 1). Older helpers are, on average, related more distantly to young they help to raise. For helpers aged 2 years or older ($n = 32$ age 2; $n = 7$ age 3; $n = 2$ age 4), only 22.0% ($n = 9$) are in a position to help raise full siblings by helping both parents breed. Most help raise half siblings or quarter siblings ($n = 24$; 58.5%) and more help breeders who are not their parents ($n = 8$; 19.5%) compared to first-year helpers (Table 1). If replacement breeders are unrelated to breeders who die, average relatedness is $r = 0.39$ for first-
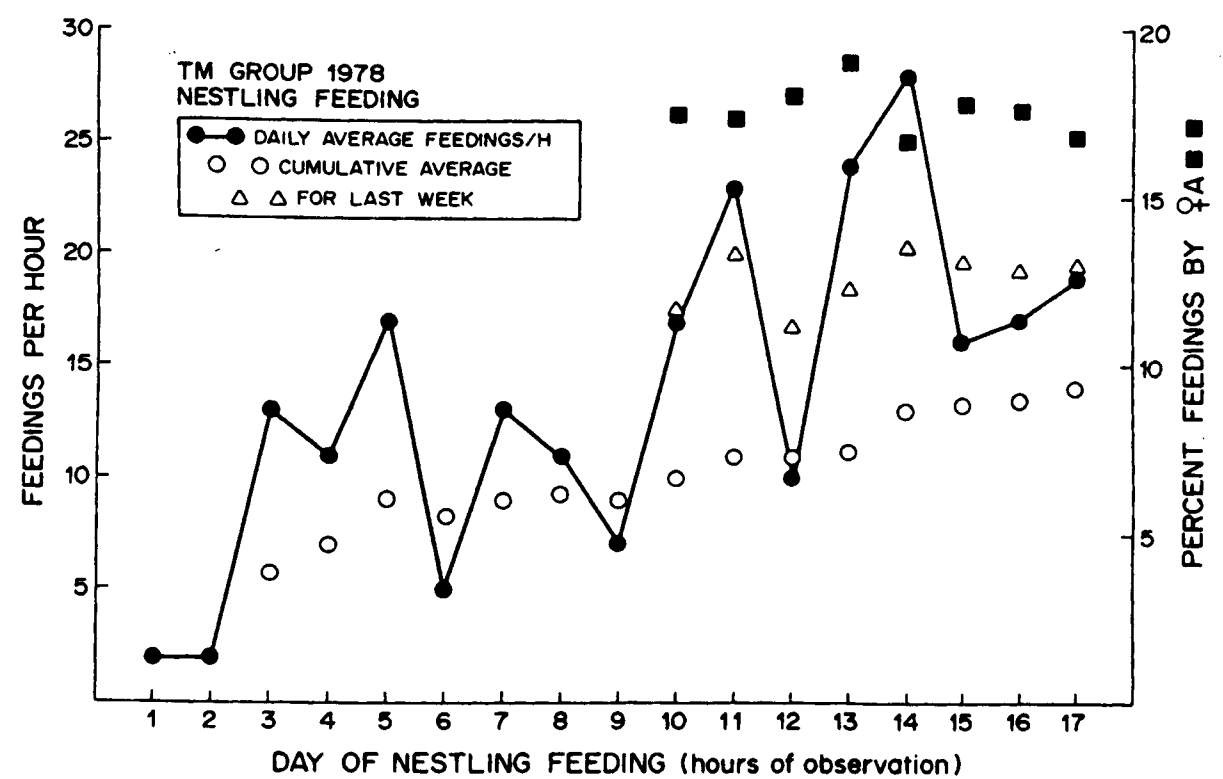

Fig. 2. The record of nestling feeding for one group from hour-long samples on each day of the nestling phase. Total feeding rates increase gradually as nestlings grow although hour-hour variability can be great. Measurements of the proportional efforts of individuals (right-hand scale) stabilize after 6 h' observation in the second week. ♀A female helper
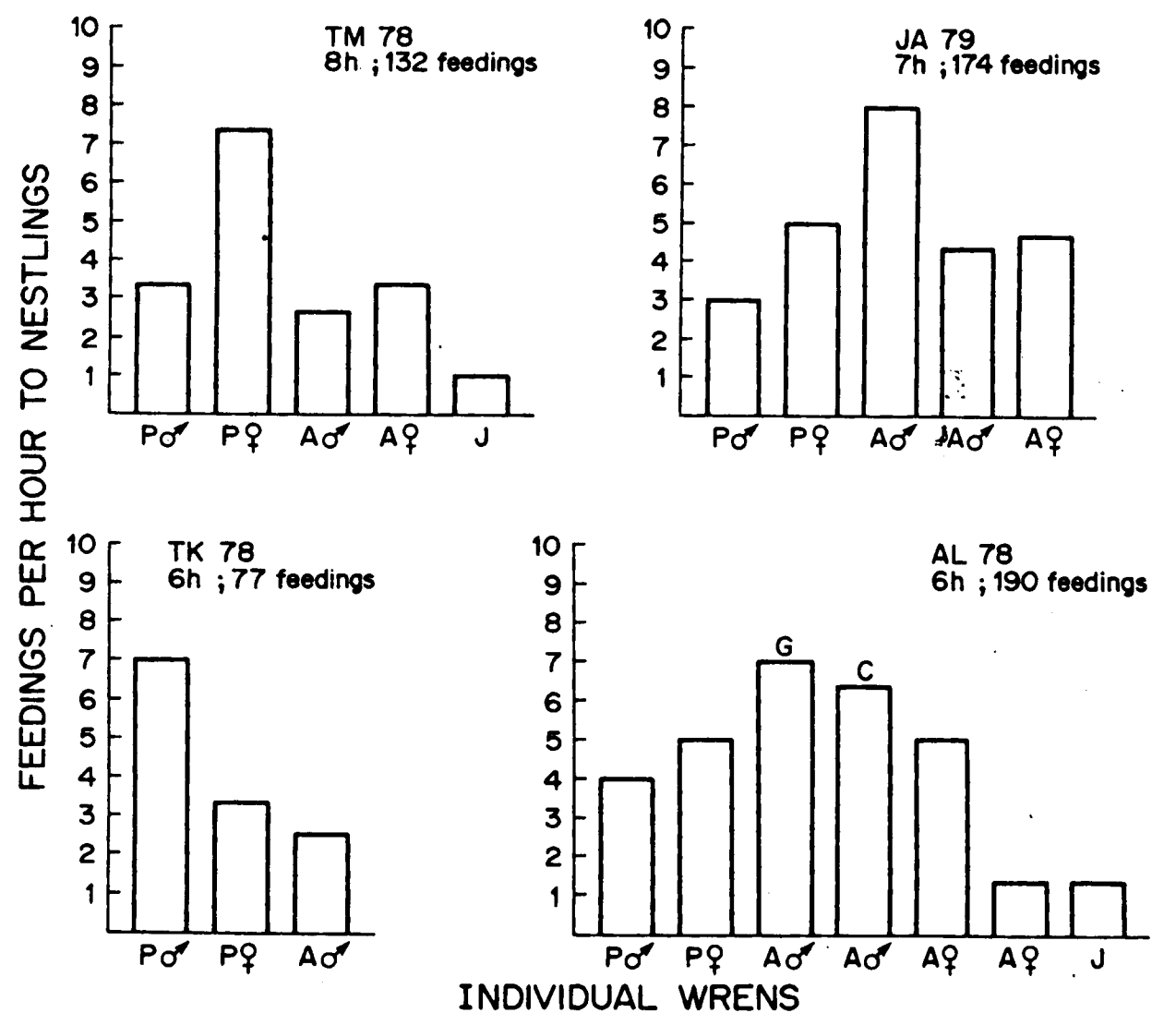

Fig. 3. Four examples of the contributions of group members to nestling feeding. Helpers (A) sometimes contribute less food to nestlings than breeders (P) (left-hand examples), sometimes more (right-hand examples)

year helpers and $r = 0.23$ for older helpers. The latter value may be inflated by the bias in the known-parentage set of helpers toward younger birds, but it is probably accurate for second-year helpers. If replacement breeders were related to helpers, even as cousins, both the average r-values reported above would be underestimates.

Direct reciprocation by helpers assisting breeders that previously reared the helper is less common in this population than offspring-parent aid. Females gaining breeding status are aided by helpers that were raised by others, except in rare

Table 1A, B. Relationships to breeders of known-parentage helpers 1978–1982

A Kinship with young being raised $(n = 151)$

	Full siblings $(r = 0.5)$	Half siblings $(r = 0.25)$	Quarter siblings $(r = 0.13)$	Nonsiblings $(r \rightarrow 0)$
First-year helpers $\bar{r} = 0.39$	73 (66%)	22 (20%)	8 (7%)	7 (6%)
Older helpers $\bar{r} = 0.23$	9 (22%)	14 (34%)	10 (24%)	8 (20%)

B Reciprocation with breeders $(n = 151)$

Helping both parents	Helping 1 parent and outside breeder	Helping ≥ 1 previous benefactor (nonparent)
82 (54%)	33 (22%)	40 (26%)

cases of females breeding in the natal territory. In 151 helper-years for known-parentage helpers, 73 cases of helping at least one non-parent were recorded. In 33 of these cases, the helper was associated with one parent and the other breeder was from another group. The remaining 40 cases show helpers aiding breeders who assisted as nonbreeders in rearing the helpers (Table 1). Most of these involved helpers aiding brothers, half-brothers or probable brothers $(n = 25)$; probable uncles $(n = 7)$; or half-sisters or probable sisters $(n = 7)$. Breeders are not often aided by birds raised with the aid of the breeder while it was a helper. For breeders with histories as helpers, in 133 bird-years breeders were aided by individuals whom they had helped to raise while helpers in only 23 cases (17%). While helpers often return the care of their parents by helping to raise siblings, they seldom reciprocate aid given them by nonparents. Breeders are most often aided by either offspring or young produced with the aid of others.

Variation in helping effort with age, sex, and degree of relatedness

Over 5 years, 56 stripe-backed wren nests in which nestlings were being fed were observed in 32 different groups for a minimum of 6 h each (total of more than 400 h). The deliveries of food to nestlings by 99 individual helpers were recorded in at least six 1-h sessions in the last week of nestling feeding. By 1981, the age and parentage of 96% of the helpers, and 45% of the breeders, in the

population were known. As a result, most of the helpers included in the analysis of helping effort are of known age and parentage $(n = 63)$. Few helpers under study have remained in their natal group long enough to experience the turnover of both breeders. However, some wrens assist in breeding attempts of unrelated individuals when (1) both parents die or leave soon after the helper begins helping, (2) the helper remains a nonbreeder long enough that both parents die in succession, or (3) the helper changes groups either in alliance with another member of the natal group or is adopted as a juvenile.

Turnover of breeders is a conspicuous event that could alert helpers that probable relatedness of the helper to any subsequent young produced on the territory has declined. This is especially true when female breeders are replaced, both because of the conspicuousness of the contest ensuing over the breeding position and because new female breeders come from outside the group and are likely to be unrelated to helpers. Helpers do not, however, reduce levels of helping after breeders change. Controlling for age and sex, helpers generally contribute as much to feeding nestlings after one or two breeder changes have occurred as they do when no such turnover has occurred (Fig. 4; no comparisons within age-sex classes across relatedness classes significant at $P < 0.05$, Mann-Whitney U-tests). Furthermore, changes of female breeders have no more effect than changes of male breeders.

Half-sibling and nonsibling helpers do not contribute less to raising young than do helpers that are full siblings to the young they are helping to raise. Full-sibling helpers (sharing both parents with the young being fed) contribute on average $\bar{P} = 0.89 \pm 0.36$ SD $(n = 28$; $P = $ proportion of an even share of feedings) to feeding nestlings, while half-siblings contribute $\bar{P} = 1.12 \pm 0.43$ $(n = 17)$ and nonsiblings contribute $\bar{P} = 1.08 \pm 0.40$ $(n = 15)$ (no differences significant at $P < 0.05$, Mann-Whitney U-tests). Adoption has been observed twice when dependent juveniles raised by small groups were incorporated into a neighboring group after one of the parents died and the natal group dissolved. In addition, a 1978 brush fire scrambled membership in 5 outlying territories without affecting mortality. As a result, several helpers aided unrelated breeding birds. In all the instances of helper transplantation into unrelated groups, the birds contributed to breeding in the foster group as energetically as any helper helping to raise full siblings in its natal group.

Because some eventually breed on their natal territories, male helpers contribute to the rearing
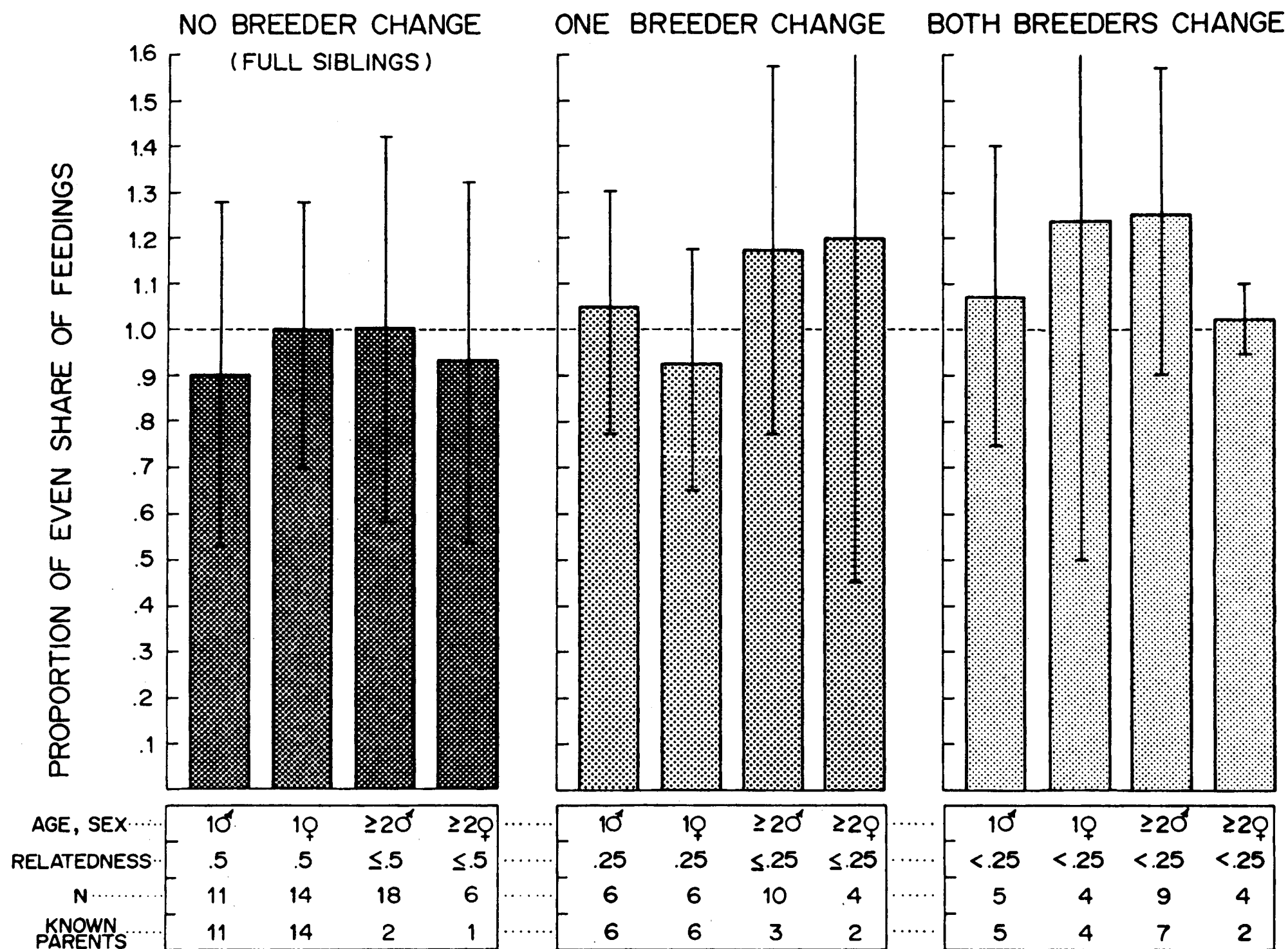
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Fig. 4. Nestling feeding by helpers with regard to age and sex of the helper, and relatedness to nestlings. Helping effort is measured as the proportion of an even share of feedings contributed by the helper (see text). The three classes of relatedness refer to the number of breeder changes since the helper was banded. For known-parentage birds (the majority), these categories translate to full-sibling recipients of feeding ($r=0.5$), half-sibling recipients ($r=0.25$) and non-sibling recipients (no parents shared, $r \to 0$, where r is the coefficient of relatedness). Within each relatedness category, helpers' effort can be compared for effects of their age (in years) or sex. Helpers' contributions do not vary significantly with age, sex, or relatedness to recipients. *Narrow black bars* indicate standard deviations

of potential helpers for themselves. However, male and female helpers' contributions to nestling feeding are very similar in spite of the fact that females will not later be helped by these young (Fig. 4). Within relatedness categories, first-year females help as much as first-year males, and older females help as much as older males (no differences significant at $P<0.05$, Mann-Whitney U-tests). Within groups, I compare helping by sibling helpers of opposite sex when age and degree of relatedness to nestlings are equal. For 25 individuals in 10 group-years, 15 dyadic comparisons were possible. In 10 cases, sisters helped more than brothers, and in 5 cases the reverse was true, revealing no tendency for either sex to help more ($P=0.15$, sign test).

Older helpers do not in general help more than younger ones in the same sex/relatedness category (Fig. 4; no differences significant at the $P<0.05$, Mann Whitney U-tests). In comparing older and younger helpers of the same sex and with identical relatedness to nestlings in the same group, 18 dyadic comparisons involving 32 individuals and

14 group-years were analyzed. In 11 of 18 comparisons, older siblings helped more than younger ($P=0.24$, sign test). In summary, all helpers tend to contribute an even share of feedings to nestlings, regardless of age, sex, or relatedness to the nestlings being fed.

One pattern does emerge from the data on helpers' contributions to the feeding of nestlings. As individual males grow older, their relative helping efforts tend to increase (Fig. 5). For 10 of 11 males whose behavior was quantified in two successive years, helping was greater in the second year ($P<0.01$, sign test). In this sample, males in the first year of observation tended to contribute less than an even share of feedings ($\bar{P}=0.93$), then increase to more than an even share in the second year ($\bar{P}=1.27$).

The immediate energetic cost of aid-giving should be measurable in the relative survivorship of individuals helping to varying degrees. I have compared survival for 46 wrens that provided less than the median level of nestling care (median $P=1.05$) to that of 45 wrens that provided more than
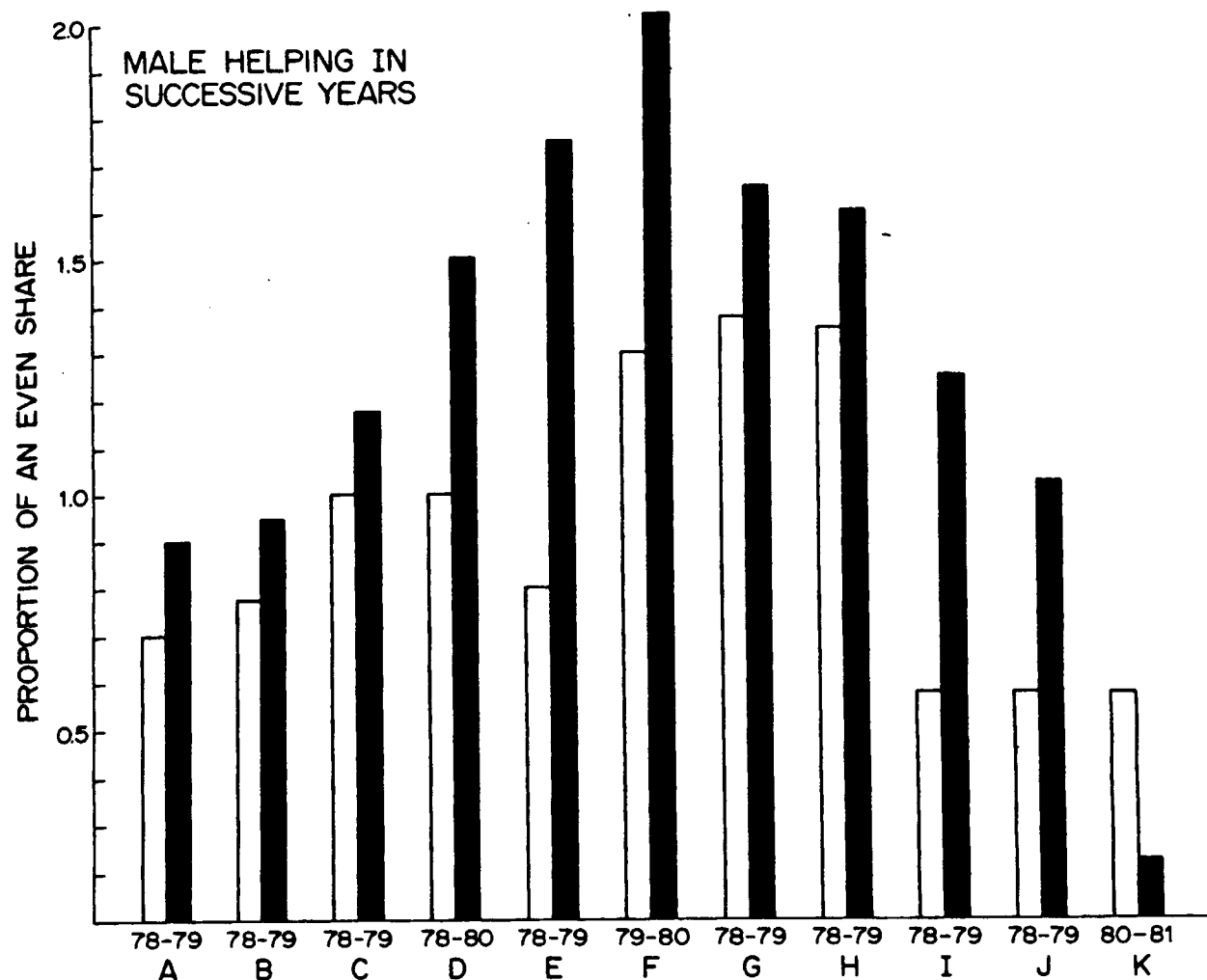
Fig. 5. Helping effort of 11 males for which helping was quantified in successive years. The *shaded bar* indicates the level of effort in the later year. In all cases but one (bird K), individuals contributed relatively more as they aged
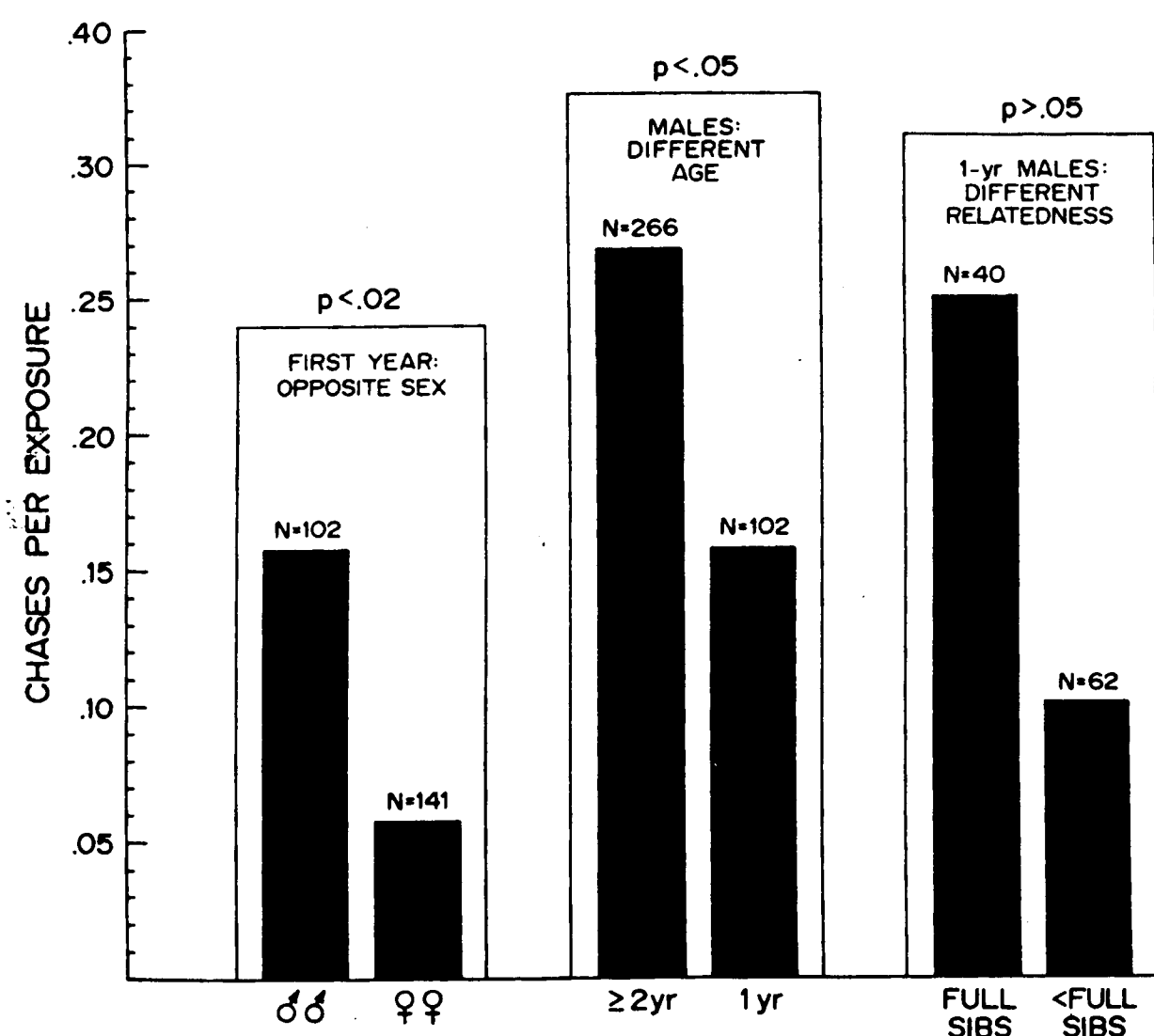

Fig. 6. Helping effort measured as chases of other species of birds from the breeding nest. Number of chases are weighted by opportunity of the class to chase (see text). Males defend more than females (*first box*); older males defend more than younger (*second box*); but full sibling helpers do not defend significantly more than half siblings (*third box*)

Nest defense

Nest defense by helpers is probably effective in improving survival of nestlings (Rabenold 1984). As an index of effort expended in defending the breeding nest, I have compiled 584 instances of wrens displacing other passerine species from the vicinity of their nest. 262 of these chases involved the brood-parasitic shiny cowbird (*Molothrus bonariensis*). The remainder were chases of thornbirds (*Phacellodomus rufifrons*), the large flycatching greater and lesser kiskadees (*Pitangus sulphuratus* and *P. lictor*), smaller flycatchers like the rusty-margined (*Myiozetetes cayanensis*), blue-gray tanagers (*Thraupis episcopus*), yellow orioles (*Icterus nigrogularis*), saltators (*Saltator coerulescens*), yellow-rumped caciques (*Cacicus cela*), and troupials (*Icterus icterus*).

In order to weight the actual number of chases recorded for a class of wrens by the opportunity that members of that class had to defend the nest, I have calculated chases/exposure. The number of chases recorded is divided by the number of times a member of the class was present when a chase occurred. First-year males chased significantly more than first-year females (Fig. 6; $P<0.02$, χ^2 test). This pattern parallels that for breeders: male breeders are the main defenders of active nests (Rabenold 1984). Older males defend the nest more vigorously than younger males (Fig. 6; $P<0.05$, χ^2-test). Controlling for both age and sex, first-year males that are full siblings to nestlings possibly have a slight tendency to chase intruders more frequently compared to half-sibling helpers (but $P>0.05$, χ^2-test; Fig. 6).

Demography and dispersal

The censuses of the study population and surroundings used to measure mortality probably miss very few living individuals. My confidence in the completeness of censuses is based on 4 major findings: (1) the number of immigrants to the population is balanced by the number of detected emigrants; (2) observed dispersal distances (presented below) within the study population are normally shorter than the distances covered in censusing away from the perimeter of the study population; (3) censusing for a full kilometer (≥ 5 territory widths) in one direction (north) from the study area, and banding and closely monitoring the groups found there, has not resulted in the detection of a single disperser into or from the study population in 6 years; and (4) only one individual

this level. Poor helpers' survival was 0.78 in the following year while the value for good helpers was 0.67 (but $\chi^2=1.54$, $0.2<P<0.3$). This suggests that if energetic helpers pay a price for their efforts in future survival, compared to poorer helpers, the price is probably not great. This issue will be explored more thoroughly in another paper.

Table 2. The balance of immigration and emigration for the study population of 30 groups in 5 years

Status of arrival	Immigrants		Emigrants	
	Male	Female	Male	Female
Breeder	3	6	3	8
Helper	1	2	0	1

recorded as deceased has ever reappeared in the study population.

In 6 years, 12 immigrants (unbanded) have arrived in the study population, and 12 emigrants have been located outside in the 30–40 groups that are censused twice each year. Most dispersal involves young females gaining breeding status outside their natal area, and the number of immigrants in this class is more than balanced by the number of detected emigrants (Table 2). These facts suggest that the censuses of individuals originating in the study population are complete.

Survivorship does not vary with group size for breeders: 0.66 annual survival in pairs and trios compared to 0.65 in larger groups ($P>0.90$, χ^2-test; $n=239$ bird-years). Only female helpers survive significantly better in large groups than in small groups (0.70 vs 0.38; $P<0.02$; all helpers: 0.74 vs 0.58; $P>0.05$, $n=283$). Survivorship does not differ for the sexes among breeders (males = 0.64, $n=119$; females = 0.67, $n=120$; $P>0.7$, χ^2-test) but male helpers survive considerably better than female helpers (males = 0.79, $n=140$; females = 0.65, $n=143$; $P<0.02$, χ^2-test) (Fig. 7). There is some tendency for females to survive slightly better in their first year than males (but $P>0.6$), but for males to survive better in the second year (but $P>0.2$). By following cohorts of wrens born in 1977, 1978, 1979 and 1980, I found that the cumulative survivorship to age 2 years is very similar for males (0.30) and females (0.22) ($P>0.3$). Females survive similarly as breeders and helpers (0.67 vs 0.65; $P>0.8$) but males survive better as helpers (0.64 vs 0.79; $P<0.01$, χ^2-test). One consequence of these demographic patterns is that the cost of delayed breeding for males, in survivorship, is less than for females. High female mortality at age two, compared to males, coincides with the normal age of dispersal from the natal group for females, suggesting a survival cost of dispersal.

Females nearly always disperse from their natal group before breeding, while most males (63%) remain to breed in the territory of their birth (Table 3). Migration between groups is usually an act
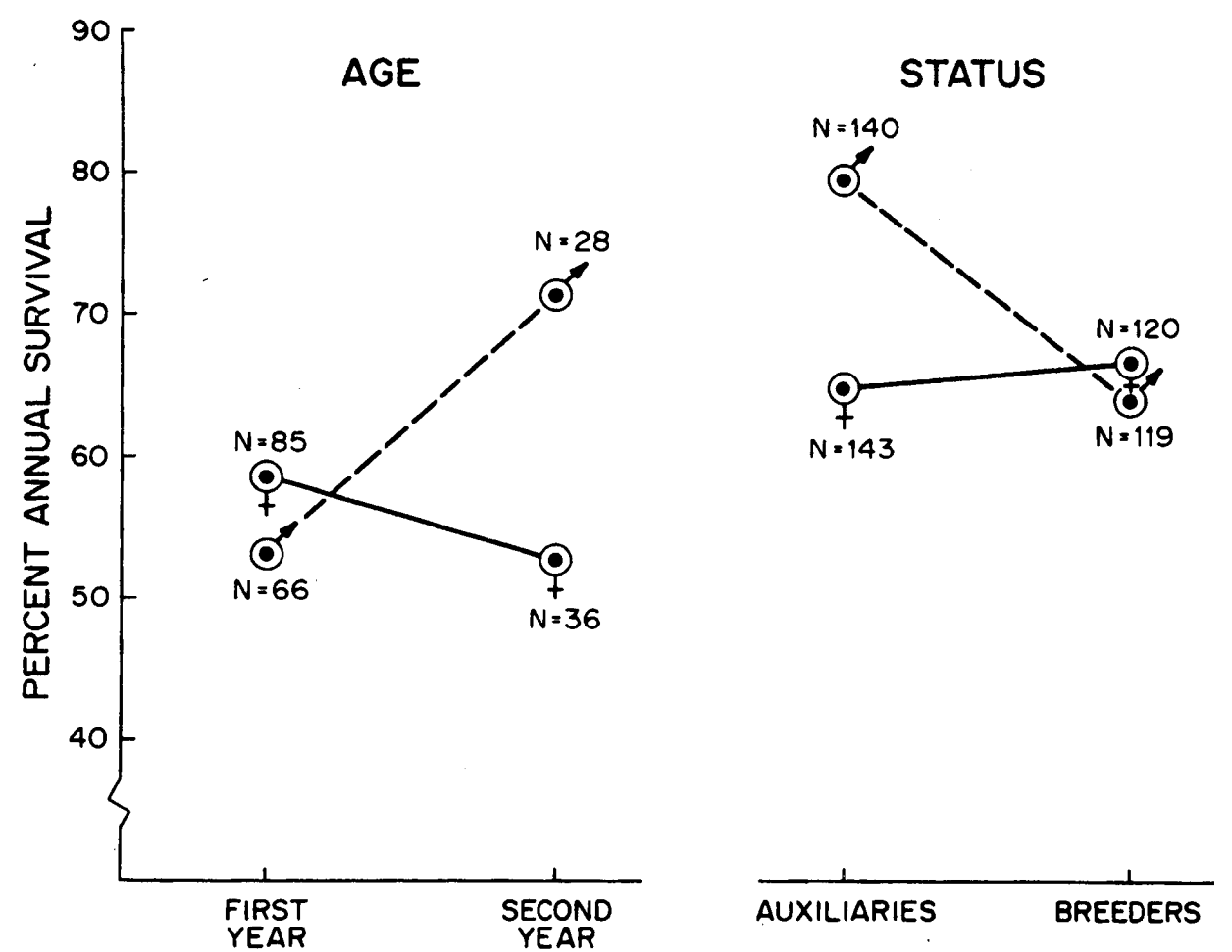
Fig. 7. Survivorship of wrens to ages one and two years comparing males and females within cohorts, and comparing the sexes for nonbreeding (auxiliary = helper) and breeding status classes

Table 3. Rise to breeding status for the two sexes with age and distance travelled. Ages are known for 20 males (57%) and 24 females (62%). Entries in parentheses are minimum values for birds of uncertain origin

	Territory on which breeding status attained				Cumulative frequency both sexes[a]
	Natal	Adjacent	1 distant	≥2 distant	
Males (n = 35)					
1 year	4	3	1		16.5 (0.22)
2 year	3 (3)	2 (1)	1 (1)		44 (0.59)
3 year	1 (6)	1 (1)		1	63.5 (0.86)
4 year	2 (1)	1			71.5 (0.97)
5 year	(1)				72.5 (0.98)
6 year	(1)				73.5 (0.99)
Females (n = 39)					
1 year		6 (2)	(1)	1	
2 year	1 (1)	5 (7)	6 (1)	1	
3 year	(1)	4 (1)	(1)		

[a] See text for explanation

of dispersal from the natal territory to breed in another; 39 females have done so in 6 years. However, nonbreeding females have on 10 occasions migrated as pairs, with one member becoming the breeder in the new group while the other took part as a helper. In 5 instances these pairs were known to be same-age sisters and in 2 cases a mother and daughter. In 11 cases, female breeders have moved to a new group while retaining breeding status; 7 had lost their mates and 2 moved from pairs to larger groups. Five breeding males transferred to breeding status in another group; 3 had lost mates. Although dispersers normally change groups only once, 2 female breeders moved from

the site of first breeding to new groups as helpers after losing mates.

Females that gain breeding status are slightly younger as a group than males: 54% of males are younger than 3 years while 82% of females are that young ($P<0.02$, χ^2). In all 74 cases listed in Table 3, the new breeder was either (a) the oldest helper of that sex in the group of origin ($n=24$), (b) a member of the oldest cohort of that sex ($n=20$), (c) the sole helper of that sex ($n=21$), or (d) assigned to a minimum age class. The frequency distribution of ages of new breeders shown in Table 3 is biased toward young ages by the minimum estimates of the ages of birds originally marked as adults. To correct for this, a cumulative frequency distribution is shown, lumping both sexes, that results from assigning half of the minimum-age entries (parentheses) to the next age category (last column in Table 3). In 33 of the 74 cases, the new breeder was known to have been the eldest of at least two same-sex helpers in the natal group. There seems to be a strict seniority system for priority to breeding status in stripe-backed wrens; a younger helper has never been known to gain breeding status before an older family member of the same sex (see also Wiley and Rabenold 1984).

Delayed breeding is the norm in this wren population, since relatively few individuals breed in their first year. In fact, at any given time, most adult individuals (≥ 1 year old) are nonbreeding helpers, since the mean group size is 5 and only 2 breed in each group. For the cohorts of 1977, 1978, 1979 and 1980, totalling 132 individuals that were raised to independent fledglings, half of them survived their first year to physiological maturity (50% of males, 60% of females). Of these surviving adults, fewer than half attained breeding status by the end of the second year after spending some time in helper status (42% of males, $n=31$; 36% of females, $n=42$). Most surviving adult wrens fail to gain breeding status by the end of their second year. The great majority of wrens in this population will never breed, since most will die first. More importantly, even among those that survive to physiological maturity, the majority commonly participate in reproduction only in the role of nonreproductive helper.

Discussion

Stripe-backed wrens live in close-knit family groups on territories that are persistent over the years. These territories are continuously occupied by male lineages infrequently invaded by immigrants. Young females eventually disperse from their natal territories to compete for breeding positions in nearby groups, and are most likely to compete successfully in immediately adjacent groups. A highly viscous dispersal pattern results. Members of both sexes belong to age-related hierarchies that establish seniority for breeding positions. The breeders in a wren group with at least two aid-giving nonbreeders enjoy considerably higher reproductive success than pairs with less help (Rabenold 1984). Nondispersal by males, a viscous female population, age-related queues for breeding positions, high productivity of juveniles relative to adult turnover, and a strong group-size constraint on successful breeding all help to determine the relative importance of kinship, reciprocation, and demography in explaining helping behavior in this system of communal breeding.

Kinship and the benefits of helping

Groups of stripe-backed wrens are usually made up of genealogical relatives, and helpers are normally the offspring of at least one of the breeders. Since aid provided to breeders in caring for young is effective in increasing reproductive success, kin selection should favor helping directed preferentially toward close relatives. Helping behavior can be favored by kin selection over attempts to breed so long as relatives produced as a result of the help are closely related and likely reproductive success following dispersal is low.

For stripe-backed wrens, Hamilton's condition for the evolution of altruism (Hamilton 1964; Michod 1982, modified for field studies by West-Eberhard 1975, and Brown 1975) is satisfied for the first few years of life in both sexes, under normal conditions. An individual should help raise the young on its natal territory if the product of the effect (additional young produced) of one additional helper, B, multiplied by r, the coefficient of relatedness of helper to young being raised, is greater than the product of probable breeding success, C (in offspring), multiplied by 0.5, the relatedness of one's own offspring:

$$rB>0.5\,C. \tag{1}$$

I assume, for wrens, that helpers do not breed and breeders do not help. If a young bird's choice for a given season is between helping in a quartet on its natal territory compared to breeding elsewhere in an unaided pair, the best choice will be clear. Unaided pairs and trios can expect to produce only 0.40 offspring/year (see Methods and Rabenold 1984) so that the right-hand side of the inequality is $(0.50)\times(0.40)=0.20$. These units can be ex-

pressed as gene equivalents (Brown and Brown 1981) or, multiplied by 2, as offspring equivalents (West-Eberhard 1975). Groups of four produce an average of 1.86 offspring/year, so that a second helper produces an increment of 1.46 offspring for the natal group. The probable relatedness of these offspring to the year-old helper is 0.25 (the relatedness of full siblings through one parent) multiplied by the probability that the mother remains alive (0.67) added to 0.25 multiplied by the probability the father remains alive (0.64). The left-hand side of the inequality is then $rB = [(0.25)(0.67) + (0.25)(0.64)]1.46 = 0.48$. For first-year wrens then, confronted with the choices of leaving their natal group of four to breed unaided compared to helping in the natal group, the latter option will on average maximize inclusive fitness since

$$rB = 0.48 > C/2 = 0.20. \tag{2}$$

This treatment assumes that replacement breeders are unrelated to helpers. If the same poor chances of breeding successfully pertained in the second year, expected relatedness to young on the natal territory would have fallen ($rB = 0.31$) but helping would still be favored. By the third year, rB will have fallen ($rB = 0.22$) to the point that breeding would be nearly equivalent to helping in inclusive fitness gain. Of course, if replacements of male breeders were uncles or half-brothers to the helper, as they often are, expected relatedness to young would never fall below 0.125 and helping in a quartet would always be a nearly equivalent option to dispersing to colonize a vacant area and breed as an unaided pair.

This simple treatment deals only with the immediate effects of a young bird's choice of two available options in a particular year. Several considerations would require a more elaborate accounting of the relative benefits of helping and breeding: (1) effects of helping or breeding could extend beyond the decision period in question, both for the subject's own reproductive potential and for that of relatives; (2) effects of helping or breeding could extend to individuals other than those most obviously affected; and (3) the breeding option is not necessarily open to a particular individual, depending on levels of competition. The rigorous framework for analysis of inclusive fitness components developed by Vehrencamp (1979) and Brown (1980, 1983) show that effects on future survival and fecundity of individuals affected by a subject's choices of breeding or helping are necessary considerations in analysis of the adaptive significance of helping. Using Brown's terminology, direct fitness components (through offspring),

present and future, and indirect fitness components (through offspring of nondescendent kin), present and future, must be considered. In the present discussion, some simplifying assumptions are warranted. For stripe-backed wrens, there is no evidence that experience in helping or breeding affects future fecundity (Rabenold 1984) and survivorship is likely more depressed by attempting to breed (including dispersal for many birds) than by helping. Few breeders are aided by young produced with their help while nonbreeders. By omitting these delayed effects, advantages of helping will be slightly underestimated. Early breeding is not likely to result in increased later fecundity, since future helpers are generally only accumulated in groups that were above the threshold of effective breeding already. Helping could also increase future reproductive potential of the helper if it contributed to dominance in competition for breeding status, but there is no evidence of this in this population. Early breeders in small groups can continue to compete for positions in large groups. Effects of helping on the future reproductive success of relatives can, however, be substantial. By contributing to the production of siblings in one year, a helper provides potential future helpers for parents or siblings breeding on the natal territory in subsequent years.

In the analysis that follows, I will modify the immediate fitness components embodied in Hamilton's inequality only by including future effects of young produced by a helper on relatives and the probability of gaining a breeding position of average productivity.

As soon as a young wren could establish itself as a breeder in a group of 4 or more adults (expected average annual production of juveniles = 2.41), it should do so even if it were thereby condemning the natal group to reproductive failure. Of course, the size of the natal group is as important in determining the relative advantage of breeding as is the size of the potential breeding group. A helper raised in a group of 7 will sacrifice no sibling production by dispersing to breed – groups of 6 are as successful as groups of 7 (Rabenold 1984). On the other end of the spectrum, the sole helper in a trio has little to gain from helping since trios do as poorly as pairs. In a population where the average group size is 5 adults and the typical group size for helpers is 4, most helpers provide effective aid in breeding, so that cessation of their aid would normally jeopardize the natal breeders' reproduction. On average, breeding in a large group (4 or more adults) would always be at least as advantageous to a young bird as helping

in the natal group, even though inclusive fitness gains from helping will normally be substantial. The critical factor favoring delayed reproduction, then, is the feasibility of gaining a reproductive position, and this is dictated by age-dependent dominance and demography.

The probability that a particular bird will be able to gain breeding status if it competes for an open position can be estimated by its age, since there is a strict seniority system for breeding status in stripe-backed wrens. Assuming 70% survivorship, a stable age distribution, and saturated breeding positions, a one-year-old helper faces competition from other nonbreeders who are likely ($P = 0.7$) to be older. If same-aged nonbreeders were on average evenly matched in competitive encounters so that 50% of a same-age cohort could be considered dominant to a particular individual, and if nonbreeders are as numerous as breeders, the chance that a 1-year-old could gain a breeding position would be only 15%, assuming dyadic competition at random. By 3 years, however, an individual stands a good chance – 59% – of competing successfully for a breeding position. This probability can be used to give a better estimate of the cost of deferring breeding by multiplying it with 0.5 C from the right-hand side of Hamilton's inequality as given in Eq. (1).

As young wrens grow older, the average potential benefits of helping fall with decreasing relatedness to young being produced in the group. In contrast, the cost of helping measured as lost reproductive potential rises as the individual's ability to successfully compete for breeding positions rises. The observed average values of r between helpers and young are 0.39 for first-year helpers and 0.23 for second-year helpers. The average increment in breeders' reproductive success attributable to helpers can be estimated by the average difference in juveniles produced per pair in groups differing by one adult member. Empirically, this value is 0.65. Average immediate, indirect benefit of helping at age one is then $0.65 \times 0.39 = 0.25$; at age two is $0.65 \times 0.23 = 0.15$. The future effects of young produced by these helpers on the breeding of relatives, after mortality (30% annually) and emigration (19% in year 1, 34% in year 2), and considering reduced relatedness in these future generations, will add 0.10 gene equivalents to the benefit of helping at age 1 and 0.06 to helping at age 2. The indirect fitness benefit of helping, including immediate and delayed effects, would then be 0.35 at age one and 0.21 at age two.

Costs of deferred breeding are determined mostly by the likelihood of successful establish-ment as a breeder. This likelihood for a particular helper will be primarily a function of its demographic neighborhood. The number of same-sex birds with seniority or greater dominance, relative to breeding opportunities, determines probability of breeding. Average reproductive success in the population is 1.43 juveniles/yr so that breeding at age one would normally produce a benefit of 1.43×0.5 [r of offspring] $\times 0.15$ [P of establishment] $= 0.11$. This value is lower than the average benefit of helping, 0.35 (from above), even if delayed effects were not considered, so that helping in this population will normally be a superior tactic to attempting to breed for year-old birds. At age two, the second potential breeding season, the average potential benefit of helping in the natal group falls to 0.21 while the cost of deferred breeding rises on average to 0.29, favoring breeding. In fact, the modal breeding age in this population is 2 years (see Table 3).

Hamilton's inequality, modified to accommodate varying probabilities of gaining breeding status, describes the extent of helping behavior in this population well, arguing that helping has been favored by kin selection. Strict age-dependent priority to breeding status and saturation of breeding opportunities strongly modify the cost/benefit balance for young helpers in natal groups. Potential breeding success that is deferred is the major cost for helpers, and this cost rises with increasing probability of successful competition for a breeding position. For a helper in a neighborhood with a high ratio of older helpers to breeding positions, gaining breeding status at a particular age will be less likely than for a helper of the same age in a neighborhood with a low helper/breeder ratio. There is some evidence for this population that wrens from neighborhoods with a high helper/breeder ratio do initiate breeding at later ages than wrens from smaller demographic neighborhoods (unpublished data).

The analysis in this discussion omits consideration of some delayed effects, especially on the subject's survival, future breeding, and some relatives' breeding prospects, that are likely more important for other species. In addition, assumptions made concerning the structure of competition for breeding positions and the annual nature of the decision process regarding first breeding may prove to be worthy of further scrutiny. Tradeoffs for males and females should also be analyzed separately. However, assumptions made generally downplay the importance of the indirect fitness component so that the conclusion that helping in the first 2 years is primarily favored by indirect fitness gain is likely

sound. A more thorough analysis will be attempted elsewhere.

The expectation of nepotism

Striped-backed wrens do not adjust helping effort according to probable genetic correlation with recipients even though reliable indicators (breeder turnover) exist. A persistent conceptual problem in interpretations of the importance of kin selection in the evolution of cooperative societies is the expectation that animals should maximize inclusive fitness by actively preferring to aid close kin rather than more distant relatives (Bertram 1976; Sherman 1977, 1980; Ligon 1981; Holmes and Sherman 1983; Blaustein 1983). Some ability to actively discriminate kin from nonkin, or degrees of relatedness, is often implied by these arguments and when helping is extended to distantly-related individuals, the conclusion is sometimes drawn that kin selection must be unimportant in the maintenance of the cooperative system (Alexander 1974; Ligon 1981; Woolfenden 1981). However, as pointed out by Maynard Smith (1976), Dawkins (1979) and Brown (1979, 1983), sophisticated powers of discrimination are not expected as concomitant of kin selection. In fact, rough "rules of thumb" could be effective in advantageously distributing aid among potential recipients, and the issue concerning optimal modifiability of these rules by individual experience is one that is separate from the question of whether kin selection contributes to the maintenance of helping behavior.

Discrimination of kin would only be useful when considerable variation in relatedness exists among potential recipients, when reliable cues about kinship are available, and when opportunities exist to redirect aid from one recipient to another or to withhold aid. In stripe-backed wren societies, young helpers are seldom confronted with begging nestlings of lesser relatedness than half siblings. In addition, when a parent is replaced by a new breeder, the helper will not likely know from direct experience whether the replacement is close kin. When mothers are replaced, they could easily be replaced by cousins from a neighboring group, but the helper will not be old enough to recognize the parentage of these individuals. Similarly, when fathers are replaced, the brother, half-brother or uncle that is the new breeder will likely be a year or two older than the helper. Most importantly, withholding aid from a replacement breeder will likely be spiteful since no opportunity will exist to redirect helping to closer kin.

Stripe-backed wrens do not move among territories to distribute aid to the closest kin. The closest kin is most likely found in the natal group even after both parents die, because of stable male lineages. The simple rule "help in rearing young in the natal territory until an opportunity arises to breed in a large group" will be more effective than attempts at further discrimination. We could conclude, then, that any kin recognition shown by stripe-backed wrens would be based on simple association (Blaustein 1983; Holmes and Sherman 1983) but these birds seem to use even simpler rules than that. As the fire that scrambled membership in 5 outlying groups showed, and as is argued by the phenomenon of adoption, acceptance into a group of wrens does not depend upon prior association. In addition, new members accepted into a non-kin group, including adoptees, helper transfers, and new breeders, do not withhold aid from begging young. Stripe-backed wrens appear to be "programmed" to feed any begging young in their group. Substantial variation in helping effort among helpers does occur, but is probably the result of sibling competition and segregation into active and subordinate social roles (this issue will be treated elsewhere). Simple "hard-wired" behavior programs, relatively closed to modification by individual experience, are probably most effective when the payoff for the particular behavior is very predictable given an identifiable set of antecedent conditions (Mayr 1974).

Dispersal patterns and patterns of tenure and replacement of breeders guarantee predictable rewards even for nondiscriminating helping behavior. Relatedness of helpers to young in the natal group will be high regardless of turnover, and higher than elsewhere. Further, aid will be predictably effective in increasing the production of related young. Similar conclusions have been reached by Brown and Brown (1980) concerning nondiscriminating aid-giving by Mexican jays. When lack of seniority prevents effective competition for breeding positions, and the energetic costs of helping do not badly erode survivorship, young wrens will be best served by automatic helping. Because helpers probably survive better in large groups (especially females), the costs of aid-giving suggested by survivorship data could be balanced by immediate survival benefits. Quantifying costs of aid-giving is hindered by the fact that nearly all helpers aid substantially in breeding efforts; there are no unhelpful helpers to use as a basis of comparison. Since males survive better as nonbreeders than as breeders, they should be somewhat less likely to take breeding options, especially the option of colonizing vacant areas.

Nondiscriminating aid-giving will only be disadvantageous when rare events place an auxiliary in a non-natal group. Of 151 known-parentage helpers observed in the last 6 years, only 8 (5.3%) occurred outside of a family group context, and only 15 (9.9%) helped raise young nonsiblings. In the absence of theoretical criteria for acceptable error levels for simple rules for aid-giving, we can only suggest empirically that the nondiscriminating aid-giving of stripe-backed wrens seems fairly efficient. Williams (1966) and Price et al. (1983) have suggested that helping behavior is simply misdirected parental care and that such mistakes have no serious selective consequences. In addition, physiologically mature animals, perhaps nearing breeding status themselves, may be "primed" to respond to begging nestlings and fledglings. Even when not strictly advantageous, counterselection against such a patently appropriate parental response may be relatively weak (Brown and Brown 1980). This sort of approach could explain the increase in helping effort as males age as well as the possibility that rearing likely future helpers becomes more advantageous as a bird nears breeding status. Helping by stripe-backed wrens cannot be considered a neutral character (Price et al. 1983), however, because it seems to carry some cost in survival and it produces a marked benefit.

Automatic or nondiscriminating helping, far from suggesting that kin selection has not played a role in the evolution of cooperation, is probably indicative of a history of predictably high inclusive fitness benefits to helpers. This is not a statement of faith, but one supported by the data on average levels of relatedness among group members. In this population, helping that is insensitive to exact degrees of relatedness is associated with (1) stable pair-bonding of breeders, (2) stable territory boundaries and group membership, (3) orderly ascension to intensely-contested breeding positions, and (4) predictably high viscosity enforced by competitive constraints on dispersal. Sophisticated powers of discrimination would probably be more advantageous in less orderly populations with higher adult turnover, more dispersal and mix among territories, unstable pair bonds, scramble competition for breeding opportunities, and more variable requirements for breeding success (poss. e.g. Emlen 1981).

Nonspecific reciprocity

Similar arguments to those preceding can be made to explain the insensitivity of stripe-backed wrens'

helping efforts to the probability that recipients of aid will one day return the favor. Female helpers are very unlikely to be later helped by the young that they help to raise, yet females provide as much aid in cooperative breeding as males. In addition, females do not often form coalitions to disperse. Of 45 females that have gained breeding status in 6 years, only 10 (22.2%) have done so accompanied by a sister or other female from the natal group. Males do not cleave off parts of natal territories to breed as in scrub jays (Woolfenden and Fitzpatrick 1978) but they can contribute to the size of the territory they could later inherit. Female helpers can contribute to their brother's future reproductive success by helping to rear future helpers for the brothers.

Specific reciprocation of aid, between former recipients and their particular benefactors, is uncommon in spite of the obvious importance overall of aid reliably provided by young helpers to breeders who once were aid-givers themselves. Aid from previous recipients is probably important in first breeding attempts. However, if breeders are counted as the recipients of aid (rather than the young being raised), then giving aid always precedes receiving aid, and recipients never reciprocate. This situation would make aid-giving very vulnerable to cheating if reciprocation between particular partners were important, as in a tit-for-tat cooperative situation (Axelrod and Hamilton 1981). However, demographics and patterns of kinship create a reliable association between young birds whose best replicative option is to participate as nonbreeding aid-givers with older breeders who offer reliable inclusive fitness rewards for helping. Each generation of yearlings will find itself in the same situation so that the helper/helped relationship between the age classes persists in spite of the absence of specific reciprocation to individual donors by recipients. This nonspecific reciprocity has been termed "indirect" reciprocity by Alexander (1979) and "generational mutualism" by Brown (1983). Stable queuing in an age-related hierarchy of priority to breeding status is critical in producing this predictability (Wiley and Rabenold 1984).

Demography, dispersal and seniority

The main demographic factors favoring cooperative breeding in stripe-backed wrens are high nestling mortality in small groups and high juvenile production in large groups relative to the low mortality of breeders. In conjunction with these demographic factors, behavioral dominance interactions

among individuals regulate age-dependency of reproduction and viscosity of dispersal patterns.

In this population, most individuals who reach two years of age participate in reproductive activities only as nonbreeding, aid-giving helpers. Very few wrens that survive one year manage to breed in that first year (13%) so that helping through at least one breeding season is nearly universal in this population. This universality of helping in young birds guarantees a newly-breeding adult in a large group a battery of helpers, whether or not the breeder had previously assisted in raising those particular individuals. Associated with the universality of helping is the stability of family-group territories and the predictability of the opportunity for helpers to contribute to the rearing of at least half siblings (79%). This predictability of both age-dependent reciprocity and inclusive fitness benefits for helpers explains nondiscrimination among kin of varying relatedness and nonspecific reciprocity. Stripe-backed wrens need preferentially help neither previous benefactors nor likely future helpers. Delayed reproduction is nearly universally advantageous as is participation in the breeding efforts of others during the nonreproductive delay. A stable social order probably favors very simple rules for aid-giving.

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