THE EVOLUTION OF COOPERATIVE BREEDING BY DELAYED RECIPROCITY AND QUEUING FOR FAVORABLE SOCIAL POSITIONS

R. Haven Wiley

Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27514

AND

Kerry N. Rabenold

Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907

Cooperative breeding, in which some members of a social group help others to reproduce, recurs as a normal feature of social organization in a variety of birds and mammals. In many cases, these helpers do not themselves reproduce while assisting in the care of others' young. How such apparently altruistic helping could evolve has been a central question in the recent development of sociobiology.

The hypotheses advanced so far fit into three general categories (Brown, 1978): (1) immediate, direct benefits for helpers, such as immediate improvement in survival or chances for breeding; (2) indirect benefits as a result of selectively helping genealogical relatives; and (3) delayed, direct benefits as a result of eventually acquiring a favorable position for breeding.

This paper focuses on the third category of explanation. The aim is to develop quantitative conditions under which delayed benefits can provide a sufficient explanation for the evolution of helping and to consider some of the evolutionary problems of delayed benefits. It is important to emphasize that the three kinds of hypotheses above are not mutually exclusive. All three effects might contribute to the evolution of cooperative breeding in a particular species or population. Indeed, it is possible that none of the three alone could provide a sufficient explanation for a particular case of cooperative breeding, whereas a combination of two or all three could.

Nevertheless, a first step is to test the adequacy of each hypothesis separately. To make these tests, we need to know the conditions under which each hypothesis can provide a sufficient explanation for the evolution of cooperative breeding.

These conditions are comparatively well formulated for the first two hypotheses. For instance, immediate, direct benefits can provide a sufficient explanation for cooperative breeding provided that each individual in a group realizes an immediate gain in fitness, either through production of young or increased survival, in comparison to its fitness when breeding alone. Immediate, direct benefits to group members play an important part in the evolution of cooperative breeding in some species (Vehrencamp, 1978). In many species, however, helpers do not reproduce, or at least have very low chances for reproduction, so that immediate, direct benefits cannot provide a complete explanation for the evolution of helping in these cases.

The indirect benefits from kin selection are also relatively well understood. Although these benefits are clearly important in the many species of cooperative breeders in which helpers join their natal groups, kin selection has nevertheless remained a controversial explanation for the evolution of cooperative breeding (Brown, 1978; Brown and Brown, 1981; Emlen, 1978, 1981; Gaston, 1978*b*; Ligon and Ligon, 1978*a*, 1978*b*, 1982; Koenig and Pitelka, 1981; Woolfenden, 1981). To determine whether or not indirect benefits can pro-

vide a sufficient explanation for cooperative breeding, we can apply an alternative form of Hamilton's condition for the evolution of altruistic behavior (Hamilton, 1964; Brown, 1978; Emlen, 1978):

$$N(g)r(g) > N(o)r(o),$$

where $N(g)$ = the expected marginal increase in the production of young by a group as a result of adding one nonbreeding helper, $r(g)$ = the expected proportion of the helper's genes shared by the group's juveniles, $N(o)$ = the expected production of juvenile offspring by an individual breeding without helpers, and $r(o)$ = the proportion of an individual's genes shared with its offspring (normally ½). This condition for the evolution of cooperative breeding, like Hamilton's original one, makes some simplifying assumptions, such as the absence of inbreeding or strong selection and additive, rather than multiplicative, effects of helping (Cavalli-Sforza and Feldman, 1978; Uyenoyama and Feldman, 1980; Feldman and Cavalli-Sforza, 1981). Nevertheless, it provides a reasonably accurate and practical condition for application to field studies of helping.

The third explanation for the evolution of cooperative breeding, as a result of delayed, direct benefits to helpers, has so far lacked quantitative formulation. The usual arguments take one of two forms: (1) by joining a group as a nonbreeding helper, an individual can eventually succeed to breeding status in that group or in a subset of the group and thereby have helpers to assist its own reproductive efforts (Ligon and Ligon, 1978a, 1978b, 1982; Woolfenden, 1981; Ligon, 1983); or (2) owing to a shortage of vacant territories in sedentary populations with high survival or, alternatively, owing to unusually harsh conditions, young individuals improve their chances of surviving and eventually breeding by remaining on their parents' territory and temporarily helping to raise younger kin (Selander, 1964; Brown, 1974; Ricklefs, 1975; Koenig and Pitelka, 1981; Emlen, 1982).

These arguments have an important

feature in common: the primary cost of becoming a nonbreeding helper in a group, in terms of the fitness of the helpers' genes, is not the immediate cost of providing help, but instead the delay before the helper can expect to have a chance to breed. The possible benefits accruing to a nonbreeding helper in a group, according to these hypotheses, are of two sorts: higher survival in comparison to that while searching for a vacant territory and a mate; and greater eventual reproductive success once the helper gains reproductive status in a group.

The possibilities for delayed benefits from helping or from remaining in the natal group are often different for males and females, since the sexes often differ in tendencies to emigrate from the natal area. In most cooperatively breeding birds and some mammals, males tend to stay in the natal group while females tend to move to other groups before breeding (Rowley, 1965; Woolfenden and Fitzpatrick, 1978; Frame et al., 1979; Koenig and Pitelka, 1981; Gaston, 1978a).

The delayed benefits of helping also depend on the order of succession to breeding status in a group. Nonbreeding helpers in a group are usually arranged in a linear ranking according to age. This ranking is discernible by careful attention to subtle interactions of helpers (Brown, 1972; Zahavi, 1974, 1976; Gaston, 1977; Stallcup and Woolfenden, 1978). It shows up clearly, however, when opportunities arise for obtaining a breeding position in a group. Then, the oldest helper normally becomes the new breeding member. Rankings are clearest among male helpers, at least in those species in which males normally attain reproductive status in their natal groups while females normally emigrate to breed.

The linear ordering of helpers might arise in two ways. One possibility is that each member of a group has a rank corresponding to its intrinsic abilities. Each newcomer would have to test itself sooner or later against the current members of the group in order to locate its proper rank.

Another possibility is that the helpers

form a queue for access to reproductive positions (Wiley, 1981). In this case, a new helper joins the tail of the queue in its natal group. In the case of males, in those species in which males usually do not emigrate from their natal groups, the helper moves to the head of the queue in the course of time and then takes the next opportunity to become a breeding member of the group. Advancement normally results from mortality of those farther ahead in the queue. Females might also form queues before emigrating to take breeding positions in other groups. In this case, the female at the head of the queue would take the next available opportunity to emigrate.

A queue differs from a ranking by contest in the way new members find their places. In a queue, order of arrival is the basis for linear ordering of individuals. Newcomers take the last position at the tail of the ordering. In a ranking by contest, each newcomer eventually takes a position determined by its intrinsic attributes independent of its order of arrival.

In cooperative breeders, the ordering of helpers results so far as known from queuing rather than ranking by contest. Since newcomers are normally individuals raised by the group, a helper's position in the queue is determined primarily by age. Only siblings of the same age have to determine their relative positions by some form of contest. As a general rule, seniority leads to priority for breeding positions (Gaston, 1977; Stallcup and Woolfenden, 1978).

The evolution of queuing behavior raises some difficult evolutionary problems. The crucial issues are the conditions that make queuing, rather than contesting for favorable positions, advantageous. Why, in other words, do not individuals in a queue try to shoulder forward or to jump the queue?

All of the foregoing features of cooperative breeding are well exemplified by the stripe-backed wren *Campylorhynchus nuchalis,* a species we have studied since 1974 in the savannas of central Venezuela (Wiley and Wiley, 1977; Ra-

benold and Christensen, 1979; Rabenold, in press *a* and *b*). Our information about this species can illustrate the use of quantitatively formulated conditions for the evolution of cooperative breeding as a result of delayed benefits to helpers. It can also illuminate the conditions that make queuing for reproductive positions advantageous. A full discussion of the relative contributions of immediate, indirect, and delayed benefits of helping will appear elsewhere.

METHODS AND RESULTS

Sufficient Conditions for the Evolution of Delayed Breeding

When individuals join groups as non-reproductive helpers, rather than seek sites for breeding elsewhere, they incur a major cost as a result of a delay in the onset of breeding. In return, they might realize benefits from greater survival and greater reproductive success at a later age. The first step in identifying the sufficient conditions for the evolution of helping by such delayed benefits is to specify the sufficient conditions for the evolution of delayed reproduction itself. Under what conditions does delayed breeding increase fitness?

It is clear that either increased survival, as a consequence of postponing reproduction, or increased reproductive success once breeding begins can help to compensate for a delay in the start of reproduction. The question thus becomes, How large is the increase in survival or later reproductive success needed to compensate fully for the effects of a delay in breeding on the spread of individuals' genes?

By using Lotka's (1956) standard equation for the rate of increase of a lineage with a stable age distribution, we can compare lineages of individuals that begin to breed at different ages (Wiley, 1981). Let one lineage include individuals that start reproduction at age a. The proportionate annual increase of this lineage, λ_1, obeys the equation,

$$1 = \sum_{x=a}^{\infty} \lambda_1^{-x} l_1(x) m_1(x). \qquad (1)$$

Here $l(x)$ and $m(x)$ are, respectively, survival and fecundity as functions of age, x.

Then let a second lineage include individuals that begin to breed at age $b > a$. In addition, in comparison to the first lineage, these individuals survive better by a factor S in all years between ages a and b and also have higher age-specific fecundity by a factor M once breeding begins. The proportionate annual increase of this lineage, λ_2, then obeys the equation,

$$1 = \sum_{x=b}^{\infty} \lambda_2^{-x} S^{b-a} l_1(x) M m_1(x)$$

$$= S^{b-a} M \sum_{x=b}^{\infty} \lambda_2^{-x} l_1(x) m_1(x). \qquad (2)$$

By separating the terms for ages a through $b - 1$ in equation (1), we can make equations (1) and (2) more comparable:

$$1 = \sum_{x=a}^{b-1} \lambda_1^{-x} l_1(x) m_1(x)$$

$$+ \sum_{x=b}^{\infty} \lambda_1^{-x} l_1(x) m_1(x). \qquad (3)$$

If lineage (2) increases faster than lineage (1), in other words if $\lambda_2 > \lambda_1$, it follows that

$$\sum_{x=b}^{\infty} \lambda_1^{-x} l_1(x) m_1(x) > \sum_{x=b}^{\infty} \lambda_2^{-x} l_1(x) m_1(x).$$

The right-hand side of this expression, we see from equation (2), equals

$$1/(S^{b-a} M).$$

Substituting this value into equation (3) and rearranging terms, we obtain the inequality

$$\frac{S^{b-a} M - 1}{S^{b-a} M} > \sum_{x=a}^{b-1} \lambda_1^{-x} l_1(x) m_1(x). \qquad (4)$$

This inequality specifies the conditions under which a lineage with delayed reproduction (lineage 2) would spread faster than one with earlier reproduction (lineage 1).

The right-hand side of this inequality expresses the cost of delayed reproduction. This cost amounts to the expected production of offspring by early breeders during the years in which late breeders have postponed reproduction, with each year's expected production weighted by its contribution to the proportionate annual increase of the lineage. The left-hand side expresses the benefits of delayed reproduction, in terms of the proportionate increase in survival during the delay and the proportionate increase in eventual fecundity.

The rate of spread of a gene favoring delayed breeding thus depends on the phenotype's increased survival and later fecundity as consequences of the delay. Note that fecundity increasing with age, regardless of when breeding begins, in no way contributes to the evolution of delayed breeding. Instead, an increase in fecundity at later ages must be contingent on the delay in the onset of breeding.

Application of the Condition for Delayed Breeding

Do helpers in a cooperatively breeding species like the stripe-backed wren meet this condition for the evolution of delayed breeding? To apply this condition, we need estimates of the fecundity and survival of individuals that breed as pairs at an early age and individuals that remain as nonreproductive helpers until they succeed to reproductive positions in groups. In practice, obtaining these estimates requires some simplifying assumptions, which we explore in more detail below.

In a population of stripe-backed wrens at Fundo Pecuario Masaguaral, 45 km south of Calabozo, Venezuela, we have marked individually all of the birds in 25–30 groups from 1977 onwards and 80% in 10 of these groups from 1974–1977. Groups include 2–10 adult wrens (at least 6 months old) and average 5.5. In each group, one pair reproduces dur-

ing the rainy season, usually between May and September. Our observations strongly suggest that other members of a group do not normally copulate or lay eggs (further details in Rabenold, in press).

Nevertheless, all members of a group participate in defending the territory, guarding the nest against predators and brood parasites, and feeding the young in the nest and after fledging. In all years, the production of independent young by pairs without helpers or with only one helper has fallen far short of that by groups with at least two helpers. From 1978–1981, groups of two or three adults produced .40 young/year ($N = 47$ group-years), while larger groups produced 2.40 young/year ($N = 49$ group-years). Production of young has not varied markedly with group size above a total of four wrens (2 breeders, 2 helpers). A full account of variation in reproductive success with group size appears in Rabenold (in press a).

Annual survival of breeding adults has averaged .64 ($N = 164$ bird-years) and has not varied with sex or size of group. Survival of helpers has averaged .61 ($N = 140$ bird-years) regardless of the size of the group. Male helpers, however, survive much better overall than do females, .78 as opposed to .47. The higher mortality of female helpers only appears after the first year and presumably results from risks associated with leaving the natal group to compete for breeding positions in other groups. Dispersal by females occurs predominantly over short distances, most often only as far as an adjacent territory. Our census procedures exclude the possibility that more than a small number of dispersing females have escaped discovery. Consequently, the low survival of female helpers after the first year must be substantially accurate. Our information so far reveals no further age-dependent influences on survival or fecundity, aside from the effects of reproductive or nonreproductive status in a group (further details in Rabenold, in press b).

These data for average survival and reproductive success permit a preliminary assessment of the sufficient condition for the evolution of delayed breeding in stripe-backed wrens. As an estimate of M, we can take the ratio of the average annual production of young by groups of at least four wrens to the production of young by pairs and trios, $2.40/.40 = 6.0$. In other words, a young bird newly established on its territory with no helpers can expect its reproductive success to reach only 1/6 the success of a bird that succeeds to reproductive status in an established group with at least two helpers. As an estimate of S, we can take the ratio of the average annual survival of helpers to the survival of breeders, $.78/.64 = 1.22$ for males. For females, after the first year of life, this value is $.47/.64 = .73$.

In addition, we need estimates of the duration of the delay in reproduction by individuals that become helpers in groups. If a young male joins a group with one older male helper in addition to the breeding male, he can expect to begin breeding at age 3 after joining the queue at age 0, provided he survives. This estimate, based on the observed mortality of males, agrees with the average age at which males in our population have attained breeding status in their natal groups, 2.7 years ($N = 35$) (Rabenold, in press b). On the other hand, one male in our study has bred successfully at the age of 1 year. Thus as estimates of a and b in inequality (4), we can take 1 and 3, respectively.

As our population has remained stable within 10% throughout our study, we can take $\lambda_1 = 1.0$ as an average over periods of several years. Note that inequality (4) includes the term λ_1, the proportionate annual increase for a lineage of earlier breeders. If in fact early breeding cannot sustain a steady population, in other words if $\lambda_1 < 1.0$, then inequality (4) with $\lambda_1 = 1$ becomes a conservative condition for the evolution of delayed breeding.

Since survival of males to age 1 is .78 but drops to .64 once males begin to breed, our estimate for the right-hand side of inequality (4) comes to
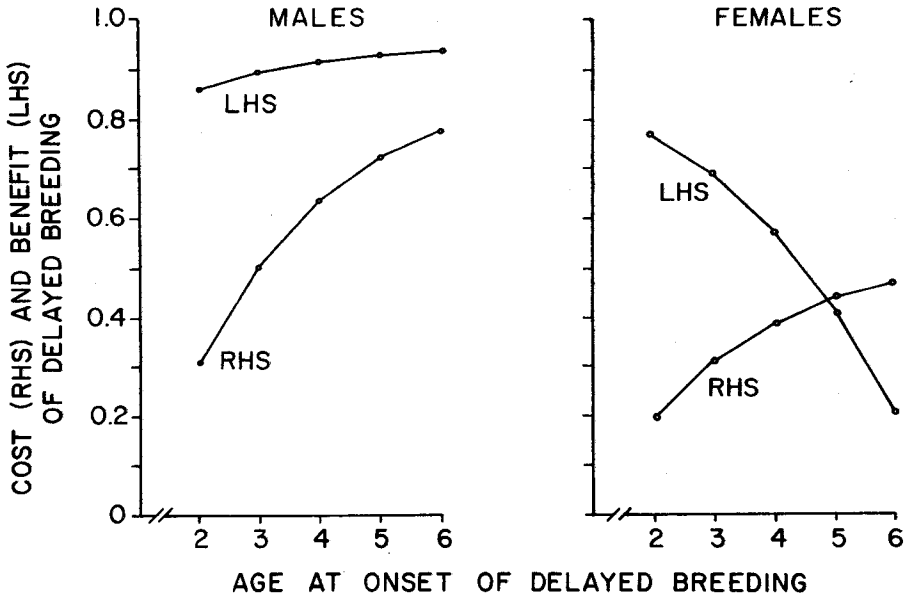
FIG. 1. Analysis of the sufficient condition for delayed breeding by stripe-backed wrens. LHS, left-hand side, and RHS, right-hand side, of inequality (4).

$$\sum_{x=a}^{b-1} l_1(x)m_1(x)$$

$$= .40(.78 + .78(.64)) = .51.$$

Our estimate for the left-hand side is substantially larger:

$$\frac{S^{b-a}M - 1}{S^{b-a}M} = \frac{(1.22)^2(6.0) - 1}{(1.22)^2(6.0)} = .89.$$

So, on average, males in this population have higher fitness if they wait in line for succession to reproductive status in a group rather than start breeding at age 1 without helpers.

For the estimates used above, it would in fact pay for males to postpone reproduction as long as necessary to obtain a reproductive position in a group. This conclusion becomes apparent when we consider that the right-hand side of inequality (4) converges on .85 as b goes to infinity, while the left-hand side converges on 1.0 (Fig. 1).

One feature of these calculations seems particularly unrealistic. Males that leave

their natal groups in their first year to establish new territories might well suffer higher mortality than males remaining in their natal groups, as we suspect is the case for dispersing females. If dispersing males have higher mortality than non-dispersers, our estimates for the right-hand side of inequality (4) are too high. This effect only increases the advantages to males of waiting for breeding positions in their natal groups rather than dispersing at age 1.

The situation is different for females in this population. Since females have lower survival as nonbreeding helpers after their first year than as breeders, our estimate of S is less than 1.0. If this lower survival results from the risks of finding and competing for a position in a new territory, then females dispersing in their first year would experience this low survival (.47) at that time but would subsequently enjoy the higher survival of breeders (.64).

For females, therefore, the right-hand side of inequality (4) amounts to

$$.40(.47 + .47(.64)) = .31.$$

Since $S = .73$ for females, the left-hand side comes to

$$\frac{(.73)^2(6.0) - 1}{(.73)^2(6.0)} = .69.$$

For females as well as males, postponement of breeding until age 3 has advantages in this population. However, since the value for S is less than 1.0 for females, the left-hand side of inequality (4) decreases indefinitely with increasing b. In contrast, the right-hand side increases to an asymptote of .51. Consequently, for females, a delay of reproduction in order to take a breeding position in a group with at least two helpers only pays to age 4 (Fig. 1). A delay to any later age does not on average increase the spread of a female's genes.

Although we have evaluated the conditions favoring deferred reproduction in each sex separately, all genes except those on chromosomes restricted to one sex would spread fastest when associated with advantageous life histories in each sex.

DISCUSSION

Simplifying Assumptions

Our sufficient conditions for the evolution of delayed reproduction are much like Hamilton's sufficient conditions for the evolution of helping behavior. Both take the form of an explicit inequality. Both involve some simplifying assumptions for application to field observations.

In most cases, our assumptions can be examined with further data. For instance, we have assumed that mortality and reproductive success beyond the first year of life vary with social position and sex but not with age or duration of breeding experience. We have also assumed that the parameters in the equation for the rate of reproductive increase are stationary in time and that the population has reached a stable age-distribution. Current information suggests that these assumptions are largely correct.

To be certain that individuals joining groups as helpers and those breeding at the same age as pairs do not differ systematically in some other way that affects reproduction or survival, it would be necessary to manipulate group size experimentally by adding helpers to pairs or small groups and removing them from large groups. Experimental removal of helpers from groups of the babbler *Pomatostomus temporalis,* a species with ecology and behavior remarkably similar to those of stripe-backed wrens (Brown and Brown, 1981; Brown et al., 1982), has demonstrated a clear effect of helpers on reproduction.

Another major assumption of our approach is that delayed reproduction and queuing are the only routes for achieving reproductive status in a large group. This assumption is borne out by our observations so far. We have so far not observed any group of two or three wrens that recruited enough young as helpers to attain the reproductive success of a large group. Although we have observed three instances of a large group splitting into two smaller ones, with consequent decreases in the reproductive success of the new groups, we have not observed the opposite, two small groups merging to form a large, successful one. Thus delaying reproduction while queuing for a reproductive position is the only way a stripe-backed wren can expect to breed in a large group.

Additional Implications of the Results

Sex Difference in Emigration.—At first sight, it appears that our results explain why females, rather than males, tend to emigrate from their natal groups, since it does not pay females to delay reproduction indefinitely. However, this difference between sexes in conditions for delayed reproduction depends on the differences in mortality of nonbreeding helpers. The higher mortality of female in comparison to male helpers apparently results from the risks of searching and competing for vacancies in neighboring groups. If the higher mortality of nonbreeding female helpers results from

searching for vacancies in other groups, it cannot help to explain why females rather than males emigrate.

Individual Adaptability. — Our analysis so far has not included the possible adaptability of individual wrens. We have instead considered whether or not an average wren in our population would do best to remain in a group as a nonbreeding helper rather than to breed with only a mate at an earlier age. Of course, few individual wrens actually confront average conditions. Natural selection should favor adaptation to particular situations, rather than to average conditions. Consider two variables that would affect the best choice for an individual wren: (1) differences in territory quality; and (2) differences in the lengths of queues for reproductive positions.

If some territories have higher expected production of young than others, owing to security from predators or to availability of food, then it would be worthwhile to wait longer for a breeding position there. M in condition (4) would be higher for helpers in good territories than for those in poor ones. If territories do differ in quality, young wrens should tend to emigrate from poor territories but to join queues in good ones.

On the other hand, a longer queue means a longer wait for a breeding position in a group. When the advantages of delayed reproduction only compensate for short delays, then a young individual should emigrate rather than join a queue likely to take too long. This consideration applies especially to females in our population of stripe-backed wrens. Although females emigrate to breed, there is nevertheless some queuing of the female helpers in each group. When a vacancy becomes available nearby for a reproductive female, several females from the same group sometimes compete as a unit for the vacancy. If they succeed, however, only the oldest female becomes the new breeding member of the group. The others return to their natal group or, occasionally, remain in the new group as nonbreeding helpers. When we recall that females in this population realize no advantage in delaying reproduction past age 4, a long queue of female helpers in a group would make it advantageous for young females to breed without helpers early in life.

For males, on the other hand, the length of the queue of male helpers in the natal group is never too long to make breeding without helpers advantageous. Young males should never leave a group to breed without helpers. Indeed, this event rarely occurs in our population.

Males might, however, choose between shorter and longer queues in groups on comparable territories. Nevertheless, young males have emigrated on only a few occasions to become nonbreeding helpers in other groups. It is possible that they simply do not have enough information about territory quality and lengths of queues to make it worthwhile to switch groups. Gathering such information might entail sufficient risks of mortality, as we see in the females, that finding and competing for the best queue does not pay.

Complementary Effects of Kin Selection. — There is of course another reason for young wrens to join their natal groups. The indirect advantages of kin selection clearly favor any tendency of wrens to become helpers in their natal groups, where the breeding pair are likely to be their own parents, at least at first.

Kin selection might have another important effect in complementing the advantages of delayed reciprocity in our population. Our analysis so far applies only to the persistence of this behavior in a population that already has established groups, not to the early spread of helping in an ancestral population.

In a hypothetical ancestral population of pairs breeding without helpers, a mutation that predisposed young wrens to become nonbreeding helpers would encounter conditions significantly different from those currently prevailing. The advantages of delayed reciprocity, although not necessarily entirely absent, are likely to be low initially. Kin selection might

then provide the essential ingredient for the initial evolution of cooperative breeding.

Relation to Other Proposals for the Evolution of Delayed Reproduction in Cooperative Breeders

The sufficient condition for the evolution of delayed reproduction emphasizes the trade-off necessary in life-history adaptations for survival and reproduction. Individuals have limited time and resources available. Furthermore, allocations of time and resources at one age constrain possibilities for allocations at later ages. Condition (4) summarizes the balance between the advantages and disadvantages of delayed reproduction in terms of these trade-offs in life-history options.

Previous explanations of the evolution of delayed reproduction and cooperative breeding have often failed to weigh these balancing options. One approach, which focuses on sedentary species with high survival, emphasizes the limited availability of vacant territories for young individuals (Selander, 1964; Ricklefs, 1975). With little chance of finding a vacancy, the argument runs, young individuals do better to stay in their natal group. This explanation, however, has an element of circularity, because the limited number of vacancies each year is a result of the existence of groups in the first place.

Imagine a comparison of two populations: one of pairs breeding on small territories each producing few young; the other of groups on proportionately larger territories producing correspondingly more young. In the first case, suppose that all individuals compete for territories in their first year, while in the second case they join groups as nonbreeding helpers. Suppose further that mortality is the same in the two populations. While the first population clearly has more individuals competing for vacant territories each year, it also has more vacancies. Indeed, if the nonbreeding helpers in groups form age-related queues for

chances to obtain reproductive positions, the ratio of the number of competitors for vacancies to the number of vacancies available would not differ for the two populations.

The behavior necessary for fission of groups and colonization of vacancies is within the capabilities of our population of stripe-backed wrens. Groups have split their territories and membership in two, and wrens from different groups have joined to establish new territories in vacant areas. Areas open for colonization, which have previously supported successful groups, have remained empty for more than a year in our study area.

To explain the evolution of tendencies for individuals to remain as nonbreeding members of their natal groups on large territories rather than to breed as pairs on correspondingly smaller territories, one cannot simply invoke a high level of competition for vacancies, even for species with high survival in relatively stable environments. Instead, it is necessary to determine the balance of advantages between finding a mate and establishing a new territory, on the one hand, and delaying reproduction, on the other.

A second approach in explaining the evolution of delayed reproduction and cooperative breeding focuses on species in fluctuating environments (Reyer, 1980; Emlen, 1982). This argument also reduces to an analysis of the balance of advantages and disadvantages for the alternatives facing young individuals. The emphasis here is on the risks of mortality and reproductive failure while establishing a new territory or finding a mate under harsh conditions. Condition (4) would allow quantitative evaluation of the consequences of delayed breeding under these conditions.

Delayed Reproduction and Delayed Reciprocity

Evolutionary advantages for delayed reproduction in stripe-backed wrens hinge on the increased reproductive success of individuals that wait to breed in a group

rather than breed at an early age as one of a pair. This increased success depends on additional helpers joining the queue behind each helper already waiting for a reproductive position. A nonbreeding male in a group thus assists in rearing future helpers that, provided he survives to breed in the group, later assist in rearing his own progeny. The helpers become the helped. This benefit from helping is a form of delayed reciprocity (Ligon and Ligon, 1978a, 1978b, 1982; Woolfenden and Fitzpatrick, 1978; Emlen, 1981; Ligon, 1983).

The problem that immediately arises is the possibility of cheating. Since giving aid precedes, perhaps by several years, the receipt of aid, why do not cheating tendencies evolve? Cheating, in this context, consists of refusing to help as a nonbreeding member of a group, but then later accepting help as a breeder.

In the special case of delayed reciprocity in cooperative breeders, cheating of this sort cannot evolve, provided two conditions are met: (1) the balance between the benefits of increased reproductive success in a favorable breeding position and the costs of any increased mortality while waiting for such a breeding position are the same for each succeeding cohort; and (2) the nonbreeding members of a group form a queue for succession to reproductive positions. Then the same conditions that make joining a group and delaying reproduction advantageous for any one individual make the same behavior advantageous for his successors. Furthermore, once an individual has joined a queue for a favorable breeding position, it then pays to raise and recruit younger individuals to join the queue behind him. Thus queuing makes it advantageous to help younger individuals, and helping (given appropriate demographic conditions) makes it advantageous to queue for succession to older individuals' positions. The interdependent advantages of queuing and helping make this reciprocity across cohorts immune to the evolution of cheating.

Condition (4) then provides more than just a sufficient condition for the evolution of delayed reproduction. In combination with stable queues for breeding positions, it also provides a sufficient condition for the evolution of cooperative breeding. The prerequisite of stable queuing, however, raises some further problems.

Queuing as an Evolutionarily Stable Strategy

Queuing, the ranking of successive individuals by their order of arrival, clearly invites the evolution of tendencies to jump the queue, to take the benefits without waiting in line for them. Under what conditions might queuing be an evolutionarily stable strategy, in the sense that no other behavioral variant can do better? In particular, what conditions might ensure the stability of queuing against variant individuals that tend to challenge opponents preceding them in the ordering?

The behavioral dynamics of queuing are potentially complex. One can imagine a variety of behavioral tactics that involve coalitions among two or more individuals against others, either to enforce queuing on disruptive individuals or to challenge individuals with greater priority. However, we have not observed any suggestions of coalitions among stripe-backed wrens in their interactions with other group members.

In the absence of coalitions, there are at least four conditions under which cheating by jumping the queue might not spread: (1) age-dependent changes in the advantages of delaying reproduction; (2) risks of losing priority as a result of contests; (3) enforcement of the current status of the queue by individuals with the highest priority and thus the most to gain in the short run; and (4) mutualistic interaction among acquainted individuals. These possibilities are not mutually exclusive.

Of these possibilities, mutualistic cooperation seems most likely to apply to stripe-backed wrens, on the basis of our

observations so far. When the individuals in a queue generate the benefits for those at the head of the queue, the payoffs for cooperating or cheating in the queue satisfy the conditions for the Prisoners' Dilemma of game theory (Rapoport and Chammah, 1965; Axelrod and Hamilton, 1981).

As a consequence of the different ages of individuals in a queue, all individuals can have the same advantages in the long run, provided they all continue to cooperate. By successfully defecting, in this case by jumping the queue, an individual obtains the benefits of reproduction in a large group at an early age and thus can increase its fitness and lower that of all other members. However, once one individual defects, all should defect, since continuing to cooperate by waiting cannot pay when others jump ahead. In this case, queuing disappears altogether, so individuals must breed as pairs with lower expected fitness than when cooperating.

As in other cases of the Prisoners' Dilemma, cooperation can spread under conditions in which tit-for-tat prevails over defecting (Axelrod and Hamilton, 1981). These conditions are satisfied when individuals recognize each other and interact an indeterminate number of times. These are just the conditions that stripe-backed wrens would face in a group. Individuals of each sex interact with each other over an indeterminate period before reaching the head of the queue and a reproductive position.

SUMMARY

The evolution of cooperative breeding, in which nonbreeding members of a group help to raise the breeding members' young, can result from one or more of three possible advantages for helpers: (1) immediate, direct advantages, such as immediate improvement in survival; (2) indirect advantages from kin selection; and (3) delayed, direct advantages for helpers that join a queue for eventual succession to an advantageous reproductive position. The conditions under which either of the first two kinds of selection can provide a sufficient explanation for the evolution of cooperative breeding are relatively well understood. We have now developed quantitative conditions under which the third sort of selection can provide a sufficient explanation.

More than one of these sources of selection are likely to influence the evolution of cooperative breeding in any particular case. Nevertheless, we need quantitative conditions under which each provides a sufficient explanation in order to understand how the three sorts of selection could complement each other.

Delayed advantages provide a sufficient explanation for helping if joining a queue for a favorable reproductive position and helping to raise the breeding individuals' subsequent young increase the spread of an individual's genes. A complete explanation thus requires conditions (1) for the evolution of delayed breeding, (2) for the curtailment of cheating among helpers, and (3) for the evolutionary stability of queuing behavior.

Delayed breeding can evolve when the eventual reproductive advantages compensate quantitatively for the delay in the onset of reproduction. For a population of stripe-backed wrens in Venezuela, this condition for the evolution of helping is satisfied for males of all ages and for females to age 4.

When helpers contribute to the increased fecundity of breeding members of groups, queuing for succession to breeding status in a group amounts to a special case of delayed reciprocity. The young that an individual helps to raise become the individual's helpers when it succeeds to breeding status in the group. In this special case of reciprocity, cheating by failing to help cannot spread, provided (1) demographic conditions favoring delayed reproduction and queuing for breeding remain the same for successive cohorts and (2) individuals queue for breeding positions.

The evolution of this form of delayed reciprocity thus requires that queuing behavior satisfy the conditions for an ev-

olutionarily stable strategy. Of several possibilities, the one most likely to explain evolutionarily stable queuing in stripe-backed wrens appears to be mutualistic cooperation among acquainted individuals.

LITERATURE CITED

AXELROD, R., AND W. D. HAMILTON. 1981. The evolution of cooperation. Science 211:1390–1396.

BROWN, J. L. 1972. Communal feeding of nestlings in the Mexican jay (*Aphelocoma ultramarina*): interflock comparisons. Anim. Behav. 20:395–403.

———. 1974. Alternate routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. Amer. Zool. 14:63–80.

———. 1978. Avian communal breeding systems. Ann. Rev. Ecol. Syst. 9:123–156.

BROWN, J. L., AND E. R. BROWN. 1981. Kin selection and individual selection in babblers, p. 244–256. *In* R. A. Alexander and D. Tinkle (eds.), Natural Selection and Social Behavior. Chiron Press, N.Y.

BROWN, J. L., E. R. BROWN, S. D. BROWN, AND D. D. DOW. 1982. Helpers: effects of experimental removal on reproductive success. Science 215:421–422.

BROWN, J. L., D. D. DOW, E. R. BROWN, AND S. D. BROWN. 1978. Effects of helpers on feeding of nestlings in the grey-crowned babbler (*Pomatostomus temporalis*). Behav. Ecol. Sociobiol. 3:1–17.

CAVALLI-SFORZA, L. L., AND M. W. FELDMAN. 1978. Darwinian selection and "altruism." Theoret. Pop. Biol. 14:268–280.

CLUTTON-BROCK, T. H., F. E. GUINESS, AND S. D. ALBON. 1982. Red Deer: Behavior and Ecology of Two Sexes. Univ. Chicago Press, Chicago.

EMLEN, S. T. 1978. The evolution of cooperative breeding in birds, p. 245–281. *In* J. R. Krebs and N. B. Davies (eds.), Behavioural Ecology. Blackwell, Oxford.

———. 1981. Altruism, kinship, and reciprocity in the white-fronted bee-eater, p. 217–230. *In* R. Alexander and D. Tinkle (eds.), Natural Selection and Social Behavior. Chiron Press, N.Y.

———. 1982. The evolution of helping. I. An ecological constraints model. Amer. Natur. 119:29–39.

FELDMAN, M. W., AND L. L. CAVALLI-SFORZA. 1981. Further remarks on Darwinian selection and "altruism." Theoret. Pop. Biol. 19:251–260.

FRAME, L. H., J. R. MALCOLM, G. W. FRAME, AND H. VAN LAWICK. 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania, 1967–1978. Z. Tierpsychol. 50:225–249.

GASTON, A. J. 1977. Social behavior within groups of jungle babblers *Turdoides striatus*. Anim. Behav. 25:828–848.

———. 1978a. Demography of the jungle babbler *Turdoides striatus*. J. Anim. Ecol. 47:845–879.

———. 1978b. The evolution of group territorial behavior and cooperative breeding. Amer. Natur. 112:1091–1100.

HAMILTON, W. D. 1964. The genetical evolution of social behavior, I and II. J. Theoret. Biol. 7:1–52.

HOWARD, R. D. 1979. Estimating reproductive success in natural populations. Amer. Natur. 114:221–231.

KOENIG, W. D. 1981. Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. Amer. Natur. 117:421–443.

KOENIG, W. D., AND F. A. PITELKA. 1979. Relatedness and inbreeding avoidance: counterploys in the communally nesting acorn woodpecker. Science 206:1103–1105.

———. 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds, p. 261–280. *In* R. D. Alexander and D. Tinkle (eds.), Natural Selection and Social Behavior. Chiron, N.Y.

LEWIS, D. M. 1981. Determinants of reproductive success of the white-browed sparrow weaver *Plocepasser mahali*. Behav. Ecol. Sociobiol. 9:83–93.

LIGON, J. D. 1983. Cooperation and reciprocity in avian social systems. Amer. Natur. 121:366–384.

LIGON, J. D., AND S. H. LIGON. 1978a. The communal social system of the green woodhoopoe in Kenya. Living Bird 17:159–198.

———. 1978b. Communal breeding in green woodhoopoes as a case for reciprocity. Nature 276:496–498.

———. 1982. The cooperative breeding behavior of the green woodhoopoe. Sci. Amer. 247:126–135.

LOTKA, A. J. 1956. Elements of Mathematical Biology. Dover, N.Y.

RABENOLD, K. N. *In press a.* Cooperative enhancement of reproductive success in tropical wren societies. Ecology.

———. *In press b.* Cooperation in breeding by nonreproductive wrens: kinship, reciprocity, and demography. Behav. Ecol. Sociobiol.

RABENOLD, K. N., AND C. R. CHRISTENSEN. 1979. Effects of aggregation on feeding and survival in a communal wren. Behav. Ecol. Sociobiol. 6: 39–44.

RAPOPORT, A., AND A. M. CHAMMAH. 1965. Prisoner's Dilemma: A Study in Conflict and Cooperation. Univ. Michigan Press, Ann Arbor.

REYER, H.-U. 1980. Flexible helper structure as an ecological adaptation in the pied kingfisher (*Ceryle rudis*). Behav. Ecol. Sociobiol. 6:219–227.

RICKLEFS, R. E. 1975. The evolution of cooperative breeding in birds. Ibis 117:531–534.

ROWLEY, I. 1965. The life history of the superb blue wren, *Malarus cyaneus.* Emu 64:251–297.

———. 1976. Cooperative breeding in Australian birds, p. 657–666. *In* H. J. Frith and J. H. Calaby (eds.), Proceedings of the XVI Ornithological Congress. Australian Academy of Science, Canberra.

SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus.* Univ. Calif. Publ. Zool. 74:1–224.

STACEY, P. B. 1979. Habitat saturation and communal breeding in the acorn woodpecker. Anim. Behav. 27:1153–1166.

STALLCUP, J. A., AND G. E. WOOLFENDEN. 1978. Family status and contributions to breeding by Florida scrub jays. Anim. Behav. 26:1133–1156.

UYENOYAMA, M. K., AND M. W. FELDMAN. 1980. Theories of kin and group selection: a population genetics perspective. Theoret. Pop. Biol. 17: 380–414.

VEHRENCAMP, S. L. 1978. The adaptive significance of communal nesting in groove-billed anis (*Crotophaga sulcirostris*). Behav. Ecol. Sociobiol. 4:1–34.

WILEY, R. H. 1981. Social structure and individual ontogenies: problems of description, mechanism, and evolution, p. 261–293. *In* P. P. G. Bateson and P. H. Klopfer (eds.), Perspectives in Ethology, Vol. 4. Plenum, N.Y.

WILEY, R. H., AND M. S. WILEY. 1977. Recognition of neighbors' duets by stripe-backed wrens *Campylorhynchus nuchalis.* Behaviour 62:10–34.

WOOLFENDEN, G. E. 1975. Florida scrub jay helpers at the nest. Auk 92:1–15.

———. 1981. Selfish behavior by Florida scrub jay helpers, p. 257–260. *In* R. A. Alexander and D. Tinkle (eds.), Natural Selection and Social Behavior. Chiron Press, N.Y.

WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1978. The inheritance of territory in group-breeding birds. Bioscience 28:104–108.

ZAHAVI, A. 1974. Communal nesting by the Arabian babbler: a case of individual selection. Ibis 116:84–87.

ZAHAVI, A. 1976. Cooperative nesting in Eurasian birds, p. 685–693. *In* H. J. Frith and J. H. Calaby (eds.), Proceedings of the XVI Ornithological Congress. Australian Academy of Science, Canberra.

Corresponding Editor: P. H. Harvey