

Genetic Consequences of Restricted Dispersal and Incest Avoidance in a Cooperatively Breeding Wren

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Can restricted dispersal in a family-structured population produce conditions that favor the evolution of helping behavior by kin selection? To address this question a numerical model of a population of cooperatively breeding stripe-backed wrens (*Campylorhynchus nuchalis*) was developed. The model incorporated the demography and social dynamics of a natural population under long-term study in Venezuela. Replicated simulations followed uniquely labelled copies of alleles for 100 annual cycles, in order to estimate coefficients of kinship between mates and between helpers and the young they raised in relation to overall levels of inbreeding in the population. The consequences of restricted dispersal and incest avoidance were investigated, under different rates of migration. The results indicated that close incest occurred too infrequently to influence genetic structure significantly. Restricted dispersal, on the other hand, even in combination with relatively high rates of immigration (10–20%), like those observed in the natural population, tended to produce genetically viscous populations. Relatedness between mates was significantly greater than 0, and relatedness among members of different groups decreased with distance. The relatedness between mates tended to increase both the relatedness of individuals to their own progeny and the relatedness of helpers to the young they raised. The latter effect predominated, so the genetic consequences of restricted dispersal, in relation to the overall level of inbreeding, tended to favor the evolution of helping by kin selection. Mutually reinforcing consequences of short-range dispersal, on the one hand, and delayed dispersal, on the other, could thus result in accelerating evolution of cooperative breeding.

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1. Introduction

In many cooperatively breeding birds, individuals regularly delay breeding beyond potential maturity and instead help to rear the young of others. Because populations of most of these species consist of groups of related individuals, non-breeders can often propagate their own alleles indirectly by helping to raise young within their group (recent reviews in Stacey & Koenig, 1990; Emlen, 1991). The magnitude of this indirect component of a helper's inclusive fitness, measured in gene equivalents, depends both on the extent to which the helper's activities increase the

group's productivity and on its genetic relationship with those it helps to raise (Hamilton, 1964; Grafen, 1984; Brown, 1987).

While measurement of group productivity is usually straightforward, genetic relationships among members of groups are more difficult to evaluate. Pedigrees from observational or genetic studies cannot provide definitive estimates of relatedness because of the inbreeding that develops in finite populations as a result of random drift. The resulting increase in background relatedness does not in itself contribute to the evolution of helping by kin selection, because all genes share the same genetic background (Grafen, 1984). As a consequence, when assessing the evolution of helping by kin selection, the relatedness of the actor to the recipient requires adjustment for the level of inbreeding in the population (Hamilton, 1972; Wade &

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Bredon, 1981; Michod, 1982; Pamilo, 1990; Queller, 1994).

This adjustment is simplified by comparing two alternatives facing an individual. For cooperative breeders, individuals face alternatives of dispersing to raise their own offspring or remaining in their natal groups to raise the offspring of the group's breeders. To estimate the production of gene equivalents in each case, the coefficients of relatedness of the actor to its own offspring and to the group's offspring both require adjustment for the level of inbreeding. As shown below, these adjustments cancel in a ratio of these two coefficients of relatedness.

Comparison of these alternatives is the central issue for understanding the evolution of helping in cooperative breeders. The principal social unit in many cooperatively breeding birds is the extended family. Males often remain in their natal groups for life, while females usually remain for some time before dispersing to take breeding positions in groups nearby (Woollfenden & Fitzpatrick, 1984; Koenig & Mumme, 1987; Rabenold, 1990; Zack, 1990). Such restricted dispersal between family groups could influence the relatedness of mates and consequently both the relatedness of individuals to their own offspring and the relatedness of helpers to the offspring they assist in raising.

Evidence concerning genetic relationships in cooperatively breeding birds has come primarily from pedigrees based on matings observed in the field or genetic analysis. Genetic analysis can clarify patterns of parentage within groups (Wrege & Emlen, 1987; Rabenold *et al.*, 1991a) and thus help to establish accurate pedigrees. Yet no analysis of pedigrees over a few generations can determine the genetic consequences of short-range dispersal and thus the genetic relationships between potential mates. Simulation by computer provides a way to address these questions for specific cases.

In this study we examined the relationship between social structure and genetic structure of a population of stripe-backed wrens *Campylorhynchus nuchalis*, based on a decade of information on the demography and social dynamics of a natural population. We compared the genetic structure of simulated populations with and without restricted dispersal. In addition, we examined two other variables that seemed likely to influence the genetic structure of cooperatively breeding populations: close (parent-offspring) incest and immigration into the population.

The simulations provided direct information on the transmission of alleles over time and the distribution of alleles within and among social groups in the population. In each run, a partially isolated population

was followed through a series of annual cycles simulating the social dynamics and demography of either the natural wren population or one with selected demographic parameters altered. Genetic structure in the simulated populations thus resulted both from the random genetic drift associated with partially isolated, finite populations and from the consequences of restricted dispersal and social structure within these populations. We asked how restricted dispersal, close incest, and immigration affect the genetic relatedness of individuals to their mates or to potential mates in other groups, to their progeny, and to the young they help to raise.

2. The Model

2.1. INTRODUCTION

The simulation, written in PASCAL (for a listing, see Stevens, 1988), followed individuals through 100 annual cycles within an area that contained sites for 36 equivalent territories, each of which accommodated no more than one group at a time. The sites formed a rhomboid with six territories per side, so that each group not on a boundary could have a maximum of six equidistant neighboring groups.

Every member of the population at the beginning of each simulation and every immigrant added later carried two uniquely labeled alleles. All subsequent progeny received at random one of the two alleles carried by each parent. A separate record for each individual stored information on its age, sex, parents, genotype and natal group. Alleles were not subject to selection. Thus, as the simulation proceeded, we could monitor genetic relationships among individuals by comparing the alleles they carried.

In the savannas of the Venezuelan llanos, clusters of territories in patches of woodland are usual for this species. For instance, from 1976–1985 the Saman population (Rabenold, 1990) consisted of 25–30 territories in a patch of woodland 0.5–1 km from the nearest other patches with this species. Within this population, reproduction and survival were not influenced by the locations of territories (Rabenold, 1984). Thus our simulation based on 36 equivalent sites for territories fits our understanding of this population.

The demographic parameters used in the simulation derive from information collected by K. N. Rabenold from 1976 through 1985 and thus do not correspond exactly to data published elsewhere based on other periods of time (Rabenold, 1984, 1985, 1990; Wiley & Rabenold, 1984, Zack & Rabenold, 1989). During this period, the Saman population increased somewhat and

then decreased, perhaps as a consequence of vegetational changes throughout the study area (Rabenold, 1990). The demographic figures used here thus represent an average over periods of increase and decrease.

2.2. SOCIAL DYNAMICS

The simulation incorporated features characteristic of the social behavior of stripe-backed wrens: delayed breeding, helping, restricted dispersal, and occasional immigration as a result of long-range dispersal. Rabenold (1990) has reviewed the social dynamics of natural populations in Venezuela. Here we summarize those features incorporated in the simulation.

Active groups contained two breeding birds (the principals) and as many as seven non-breeding birds (auxiliaries) of both sexes, either helpers or juveniles. Access to breeding positions depended on a system of queuing (Wiley & Rabenold, 1984). For every group, the simulation maintained separate queues for auxiliary males and females. Each juvenile entered the bottom of the appropriate queue in its natal group at birth and remained in the queue until it died, secured a vacant breeding position or, rarely, joined a neighboring group as an auxiliary. Birds advanced in the queues as those above them died or dispersed to take breeding positions. Except in a few cases mentioned below, breeding by each individual was delayed until it rose through the queue for its sex and became a principal in a group.

Queuing assured that the oldest auxiliaries in groups filled vacancies. The simulation selected a new principal female at random among the oldest auxiliary females in other groups. To simulate the natural population, a female's probability of dispersal depended on proximity to the group with a vacancy. Most females (80%) came from a neighboring group. Less frequently, females dispersed a distance of two territories (15%) or farther (5%).

Breeding vacancies for males, as in natural populations, were usually filled from within the group. Normally the oldest auxiliary male assumed breeding status. Occasionally, when a group lacked an auxiliary male, an auxiliary male from a neighboring group filled the vacancy. In the simulations, all-female groups of three or more (those potentially at or above the threshold for reproductive success in this population, as explained below) always attracted a male, while smaller all-female groups did so only in a small proportion of cases. Failure to attract a male led to dispersal or death of the females in these groups. Because most dispersing males in the natural population had low rank in their natal territories, the simulation selected third-ranked auxiliary

males for dispersal in these cases. As with females, dispersal probabilities were weighted by distance, and dispersal distances greater than one territory were infrequent.

In the natural population, successful reproduction never occurred when a male succeeded to breeding status in his natal group while his mother was still the breeding female. In these cases, the mother always disappeared or dispersed. Consequently, our simulations of the natural population prohibited mother-son incest by requiring the mother in these cases to disperse or die.

Auxiliaries had one other option for obtaining a breeding position: they could colonize unoccupied sites. Colonization occurred only by fission of very large groups, as happened occasionally in the natural population.

2.3. DEMOGRAPHY

Each annual cycle in the simulation included the following sequence of demographic events: mortality, dispersal and breeding. This approximated the seasonal phases of the natural population of wrens, in which highest mortality occurred during the non-breeding season. In the simulations, all breeding vacancies arose during the mortality phase and were filled during the following dispersal phase. The vacancies were filled in order of group size, from largest to smallest, in accord with the observed preference of dispersers for larger groups (Zack & Rabenold, 1989).

Survival in the simulations matched observed values for the age, sex, and social status of birds in the Saman population from 1976-1985. No adjustment was made for possible inbreeding depression. Maximum age was set at 12 years, the maximum age observed in the field. Annual survival rate was higher for female principals (68%) than for male principals (62%). Oldest auxiliary females, which competed for vacant breeding positions, had the lowest survival rate (65%) among auxiliaries. Annual survival of other auxiliaries regardless of sex was 81% for the first year and 79% thereafter.

The simulation incorporated a pronounced threshold for reproductive success as a function of group size to match that observed consistently in the natural population. Only 23% of pairs and trios successfully produced a first brood, while groups with two or three helpers were three times as successful (69%). Additional auxiliaries beyond the first three raised the probability of success to 88%. Groups fledging young in any one annual cycle also had a size-specific probability of fledging a second brood. Pairs and trios were never successful, groups with four or five auxiliaries succeeded 25% of the time,

and larger ones were successful with second broods 40% of the time. Successful nestings produced from one to four fledglings in the same proportions as in the natural population. The model imposed a maximum group size of 16. By constraining the number of young produced by larger groups to conform with this limit, the simulation introduced an element of density dependence. All of these features of the simulations matched those observed in the natural population.

2.4. VARIABLES: IMMIGRATION, RESTRICTED DISPERSAL AND INCEST

The simulations compared five rates of immigration. In each annual cycle, 0, 5, 10, 20 or 40% of breeding vacancies were allocated at random to immigrants with new alleles and thus with no genetic relationship to current members of the population. Immigration into the 25–30 groups of the natural population was low, averaging approximately one bird per year or about 10–15% of breeding vacancies. Mortality rates, both in the field and in the simulation, included low rates of emigration.

The simulations also compared three different social conditions, each combined with the five levels of immigration. The first condition (*NP*, *Natural Population*) matched the natural situation: mothers and sons did not mate, and oldest auxiliary females dispersed primarily to neighboring groups, as specified above. The other two social conditions allowed us to assess the consequences of close incest and random dispersal. The second condition (*IA*, *Incest Allowed*) allowed matings between mothers and sons but retained the restricted dispersal of the *NP* condition. The third condition (*RD*, *Random Dispersal*) allowed matings between mothers and sons, as in the *IA* condition, and also allowed the oldest auxiliary females to disperse randomly within the population to assume breeding positions.

3. Methods

3.1. STARTING CONDITIONS AND SAMPLING PROCEDURES

The starting population for every run consisted of 20 groups in the same set of locations selected randomly at the outset. Measures of population inbreeding and relatedness were calculated at 10-year intervals for four social relationships (male and female principals, female principals and their young, oldest auxiliary females and the young in their groups, and oldest auxiliary females and males in neighboring groups). Each group initially contained five birds (two 4-year-old breeders and three 3-year-old auxiliaries, one male and two females), slightly less than the

average of 5.5 for the natural population but above the threshold for successful reproduction. Each of the 100 birds received two alleles. We computed 100 runs for each set of conditions, simulating 100 separate populations all starting with the same initial conditions, and calculated summary statistics (referred to below as overall means and variances) across all populations. For all statistical comparisons, we used *t*-tests for large samples, with $\alpha = 0.05$, unless otherwise specified.

3.2. MEASURES OF RELATEDNESS AND INBREEDING

The measures of genetic similarity presented here are overall means for the probability that homologous genes drawn from each of two individuals (*i* and *j*) were identical by descent. Since all genes in the population descended from uniquely identified genes in the starting population, or from those carried by immigrating females, genes having the same identification label were identical by descent. When averaged within a population, these measures of similarity represented the coefficients of kinship (Crow & Kimura, 1970).

We measured inbreeding in two ways. The proportion of individuals with genes identical by descent gave an exact measure of population inbreeding (*F*). The average coefficient of kinship for mates (the breeding principals in each group) provided an estimate for *F*. The two should be the same in standard pedigree analysis (Crow & Kimura, 1970).

3.3. KIN SELECTION OF HELPING BEHAVIOR

To obtain sufficient conditions for the evolution of helping by kin selection, we can apply Hamilton's (1964) general condition for the evolution of altruistic behavior to the alternatives for non-breeding members of groups (Brown, 1978, 1987; Emlen, 1978; Grafen, 1984). In a comparison of these alternatives, delayed dispersal and helping must yield greater inclusive fitness, measured by production of gene equivalents (Brown, 1987), than immediate dispersal and breeding, as follows:

$$Gr_H - Lr_B > 0,$$

where *G* = the number of additional young produced by a group as a result of the helper's presence (the gain for an individual that stays and helps); *r_H* = the coefficient of relatedness between an individual and the additional young produced by its group if it stays and helps; *L* = the number of young produced by breeding without helpers (the loss for an individual that stays and helps); and *r_B* = the coefficient of relatedness between an individual and the young produced if it disperses and breeds without helpers. In age-structured

populations, coefficients of relatedness require adjustment when recipients of help differ in age (Charlesworth & Charnov, 1981). These adjustments were not needed in our calculations, as all recipients are the same age (newly produced young).

To examine how genetic structure affected kin selection for helping behavior, we focused specifically on the oldest auxiliary females in groups of four. Since helpers in groups of four produce the greatest marginal increase in group productivity, the immediate benefits of delayed dispersal and helping are maximal in this case. Furthermore, the oldest auxiliary females provide the crucial test, because they stand to gain the least from helping. As auxiliaries grow older, the chance that one or both of their parents has died increases and their relatedness to the young they help to rear decreases. Meanwhile, their chance of obtaining a breeding position increases, because older females compete more effectively for vacancies, all else equal (Zack & Rabenold, 1989).

We can rearrange the inequality above into the more useful form $G/L > r_B/r_H$. The value G/L has already been determined for the Saman population. Females assisted by at least two helpers produced on average 1.77 young, while females assisted by one or no helpers produced 0.40 young (Rabenold, 1984). Thus G/L , the ratio of the mean increase in number of offspring produced by groups with two helpers (1.77 - 0.40) to the mean produced by groups with one or no helpers (0.40) was 3.43.

The value r_B/r_H poses two problems. First, the coefficient of relatedness is required, not the coefficient of kinship as measured in the simulations. Based on pedigrees, the two are related in the following way (Hamilton, 1972; Pamilo & Crozier, 1982):

$$r_{ji} = 2f_{ij}/(1 + F_i),$$

where r_{ji} = the coefficient of relatedness of recipient (j) to helper (i) (the probability that any one gene in i is identical by descent [i.b.d.] to a gene in j); F_i = the inbreeding coefficient of the helper; and f_{ij} = the coefficient of kinship between helper and recipient (the probability that two homologous genes drawn from i and j respectively are i.b.d.). Note that the r values calculated here are adjusted for the inbreeding level in the population.

Substituting for the two r values in the inequality above, and noting that F_i is the same in both cases, the right-hand side of this inequality reduces to

$$r_B/r_H = r_{B_i}/r_{H_i} = f_{B_i}/f_{H_i},$$

where r_{B_i} = the coefficient of relatedness between an

oldest auxiliary female (i) and the young (B) she could raise if she bred on her own; r_{H_i} = the coefficient of relatedness between an oldest auxiliary female (i) and the young (H) she helps raise; and f_{B_i} and f_{H_i} = the corresponding coefficients of kinship. The adjustments for overall level of inbreeding in the population cancel, so that, regardless of inbreeding level, a ratio of coefficients of kinship can substitute for a ratio of coefficients of relatedness.

The second problem arises because matings involving oldest auxiliary females are hypothetical; no direct measurements are possible of their coefficient of kinship with actual mates or with young they actually produce (f_{B_i}). We cannot assume $f_{B_i} = 0.25$ when mates are often relatives, as is likely when populations are finite or dispersal restricted. To estimate f_{B_i} , we first calculated the average coefficient of kinship between oldest auxiliary females and all the males in adjacent groups. We then used this figure to estimate the expected coefficient of kinship between oldest auxiliary females and the young they would produce by mating with one of these males at random. Note that by choosing a mate in an adjacent group a female's expected r_B will be higher than if she chooses a mate at random, so the critical ratio r_B/r_H will be higher. This case thus represents the crucial test for the evolution of helping as opposed to dispersing.

4. Results

4.1. GENERAL

In many ways the behavior of the simulated populations fit qualitative expectations for finite populations subject to different rates of immigration and different patterns of dispersal and close incest. However, the influences of restricted dispersal on genetic structure persisted under surprisingly high rates of immigration by unrelated individuals. We review the results for the relatedness between specific categories of individuals in the population before considering the crucial relatedness ratio.

The numbers and sizes of groups in the simulated populations varied around the values for the natural population. As expected for partially isolated populations, a proportion of our replicates did not persist the entire 100 annual cycles (Table 1). Both immigration rates and social conditions influenced the proportion surviving, presumably through their interacting influences on the sizes of groups (Table 1). The numbers of active groups and the mean sizes of groups after 100 annual cycles in the simulations with conditions closest to the natural population

TABLE 1
Characteristics of active groups remaining in the simulated populations after 100 annual cycles

Social conditions†	Immigration rate	Persisting populations	Mean number of active groups	Mean group size‡
NP	0%	47	17.5	6.7
	5%	84	24.3	8.2
	10%	89	27.9	8.6
	20%	87	26.9	8.5
	40%	99	33.8	11.0
IA	0%	71	23.1	7.8
	5%	86	21.2	8.0
	10%	86	27.4	8.2
	20%	97	30.8	9.6
	40%	99	35.1	11.9
RD	0%	59	19.0	7.0
	5%	69	22.0	7.4
	10%	71	26.0	7.9
	20%	94	29.7	9.1
	40%	99	34.7	11.7

† NP, social dynamics and demography like a natural population; IA, like preceding but with close incest allowed; RD, like preceding but with random female dispersal within the population.

‡ Following the breeding season, thus including young of the year.

(NP with 10–20% immigration) were somewhat higher than those actually observed in the Saman population from 1976–85. Nevertheless, the simulations generated populations that did not deviate much from the natural population.

4.2. RELATEDNESS OF MATES

As expected, average relatedness between the two breeders in a group quickly increased for all runs of the simulations. By year 30 for all combinations of

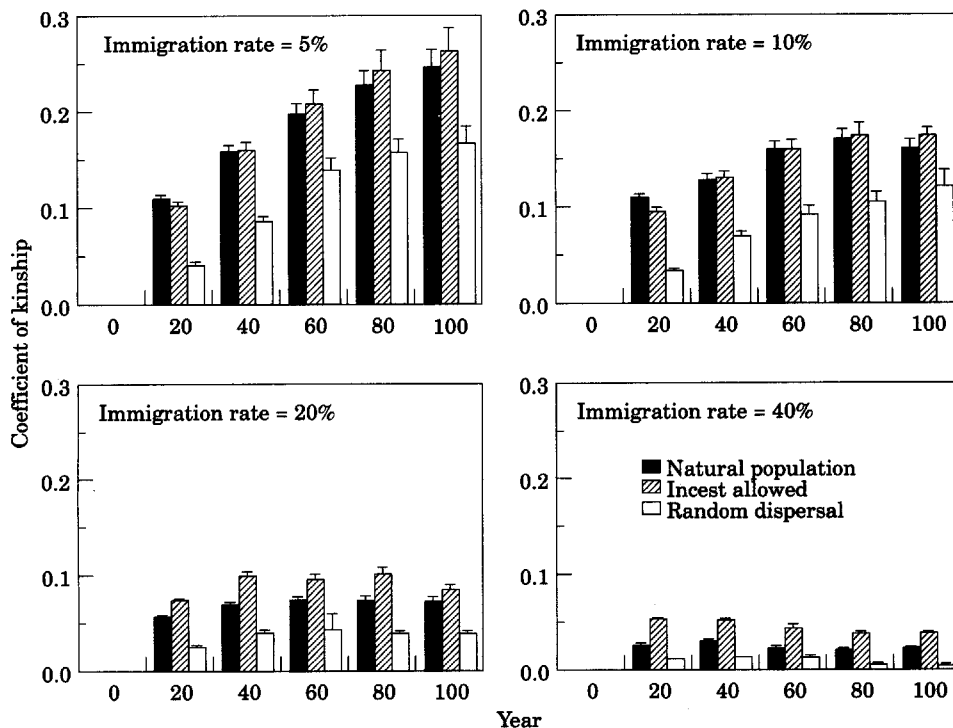


FIG. 1. Overall mean coefficients of kinship (f) between mates (principal male and female in a group) during the course of 100 annual cycles in simulated populations. We compare four rates of immigration and three social conditions (Natural Population, NP; Incest Allowed, IA; and Random Dispersal, RD; see text for details). The vertical line on each bar represents one SE ($N = 100$ replications). The absence of a vertical line indicates a SE too small to resolve at this scale.

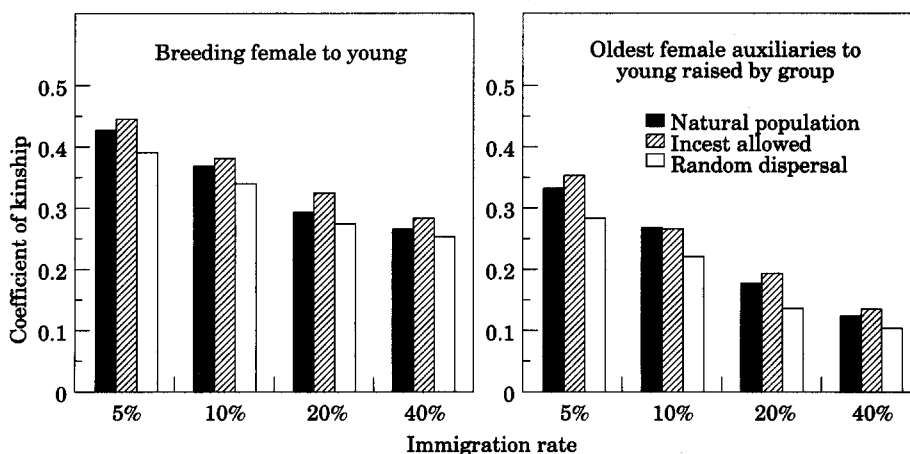


FIG. 2. Overall mean coefficients of kinship (f) between breeding females and their young (left) and between oldest female auxiliaries and the young they help to raise in their natal groups (right) after 100 annual cycles in simulated populations. See Fig. 1 for further explanation.

parameters, mates were more closely related than expected for random mating in a large population (Fig. 1). In all cases, inbreeding coefficients closely matched the coefficients of kinship between mates. At no time did these measures, or their variances, differ significantly. Consequently, in the following sections we present only coefficients of kinship as measures of relatedness.

Also as expected, relatedness of mates was inversely related to immigration rate under all three social conditions. In closed populations (0% immigration), kinship increased almost linearly as a result of continual loss of alleles. In contrast, relatedness stabilized after 20–40 years of high immigration (20 and 40%). Intermediate rates of immigration (5 and 10%) resulted in relatedness values that tended toward, but never completely attained, stability by the end of 100 annual cycles. For each of the three sets of social conditions, relatedness between mates was always significantly greater than zero after year 30.

Close incest increased average relatedness between mates in two ways. First, a small proportion of potential pairs were mothers and sons, a mating combination prohibited under NP conditions. Second, these matings reduced turnover of breeding females. Even though incestuous matings never averaged more than two per year, and were usually half that, fewer vacancies meant fewer opportunities for female dispersal and immigration. The consequences were slight in the IA condition when most replacements came from within populations. Thus only for the highest immigration rates (20 and 40%) were there significant increases in relatedness as a consequence of close incest.

As expected, random dispersal of females to fill breeding vacancies (condition RD, Fig. 2) significantly

reduced relatedness between mates at all times after year 30, for all immigration rates. Random dispersal of females, however, did not completely eliminate the genetic structure of the simulated populations even with immigration rates as great as 40%. In addition to finite population size, several features of social behavior tended to maintain elevated relatedness of mates, even when females dispersed randomly. These features included infrequent close incest, restricted dispersal by males, and clustering of active groups. Although male dispersal occurred infrequently, constraining it to adjacent territories contributed to genetic similarities between neighboring groups. Clustered groups, particularly if one or more were large, tended to exchange dispersers repeatedly. In addition, just as in natural populations, larger groups produced most of the dispersing females that filled nearby breeding vacancies.

4.3. RELATEDNESS OF OLDEST AUXILIARY FEMALES TO THE YOUNG THEY HELP TO RAISE

Increases in relatedness between mates were paralleled by increases in relatedness both between mothers and young and between oldest auxiliary females and young. In our simulations, these categories of relatedness reached stable values within ten annual cycles. Consequently, we present only the values at the end of 100 cycles (Fig. 2).

Whatever the level of immigration, and consequently inbreeding, in a population (measured as the coefficient of kinship between mates), oldest auxiliary females were approximately half as closely related to young they helped to raise as were the mothers of the young. For example, for the RD condition with 40% immigration, the relatedness of oldest auxiliary females to the young they helped to raise was 42%

(0.105/0.253) of the relatedness of the mothers to these young (Fig. 2). The ratio was slightly less (40%) when we subtracted the inbreeding level in the population from each relatedness in order to obtain a measure of relatedness in excess of that expected from inbreeding alone. At lower immigration rates, ratios of the excess relatedness of oldest auxiliary females and mothers to young showed the same patterns. After adjustment for the inbreeding level in a population, oldest auxiliary females were somewhat less than half (41–50%) as closely related to young as were the mothers of these young.

This stability was a consequence of the patterns of replacement for breeders. The longer an auxiliary remained in her natal group, the more likely it was that her mother had died and been replaced by a breeding female from outside the group. This replacement changed an auxiliary's relationship by pedigree to subsequent young in the group from siblings to half siblings. Replacement of the breeding male had less influence on an auxiliary's expected relatedness to young, because the replacement for her father was likely to be one of her brothers. On the other hand, further replacements of the breeding female would have little effect on an auxiliary's relatedness to young in the group, because subsequent female breeders were all recruited equivalently from outside the group. The relationship of an auxiliary female to young in her natal group would thus shift at some point in her life from siblings to half siblings (or to nieces/nephews of equivalent relatedness) and then remain relatively stable.

Note that the expected age of an auxiliary at the time of this shift would decrease with increased turnover of female breeders as a result of mortality. Increased turnover of breeders would also decrease the expected residence time of a female auxiliary in her natal group. Consequently, there is little net effect on the relatedness of oldest females to the young they raise.

In the Saman population, just as in the simulations, oldest auxiliary females helped to raise young that were roughly their half sibs or genetic equivalents (Rabenold, 1985, 1990). The simulations have emphasized the stability of this pattern of relationships despite alterations in immigration rates and some social conditions.

4.4. RELATEDNESS OF OLDEST AUXILIARY FEMALES TO MALES IN NEIGHBORING GROUPS

The farther oldest auxiliary females dispersed to secure vacant breeding positions, the less related they were on average to their new mates. Relatedness always decreased significantly with distance for all immigration rates under all sets of social conditions

(Fig. 3, $P < 0.001$, t -tests for regression coefficients). As expected, the correlation with distance was significantly greater when dispersal of females was restricted (conditions NP and IA versus RD; $P < 0.05$, t -tests for regression coefficients with equal variances). Close incest had no significant effect on the genetic correlation with distance (conditions NP versus IA; $P > 0.05$, t -tests like the preceding).

Relatedness between oldest auxiliary females and males in groups one territory away closely paralleled relatedness between mates but was usually slightly higher (compare Figs 1 and 4). In the absence of immigration, this greater relatedness between future than between current mates simply reflected the continuing loss of alleles. Since immigrant females were unrelated to the breeders in the population, high immigration rates (20 and 40%) increased the difference between the relatedness of mates and that between oldest auxiliary females and males in neighboring groups (differences significant after year 30).

With close incest allowed (IA condition), the reduction in relatedness between mates as a result of immigration was balanced by increased relatedness resulting from matings between mothers and sons. In this situation, except for years 30–50 at an immigration rate of 20%, the relatedness of oldest auxiliary females to males in neighboring groups did not differ from the relatedness of mates.

4.5. RELATEDNESS RATIO AND SUFFICIENT CONDITIONS FOR KIN SELECTION

Any conditions that lowered the relatedness ratio, r_B/r_H , for oldest auxiliary females would relax the ecological conditions (G/L) for the evolution of helping by kin selection. In the simulations, relatedness ratios varied with immigration rate and social condition (Fig. 5). Close incest in most cases significantly reduced relatedness ratios relative to those in the natural population, while random dispersal in every case significantly increased these ratios by comparable amounts.

Of course immigration also affected relatedness ratios. With no immigration, relatedness ratios declined inexorably toward a ratio of 1.0, the necessary result for a genetically uniform population. For immigration rates of 5 and 10%, the relatedness ratio approached stability at some level above 1.0. At higher immigration rates, the relatedness ratio remained nearly stable (20% immigration) or increased with time (40% immigration).

Under social conditions resembling the natural population (NP), r_B/r_H for oldest auxiliary females and

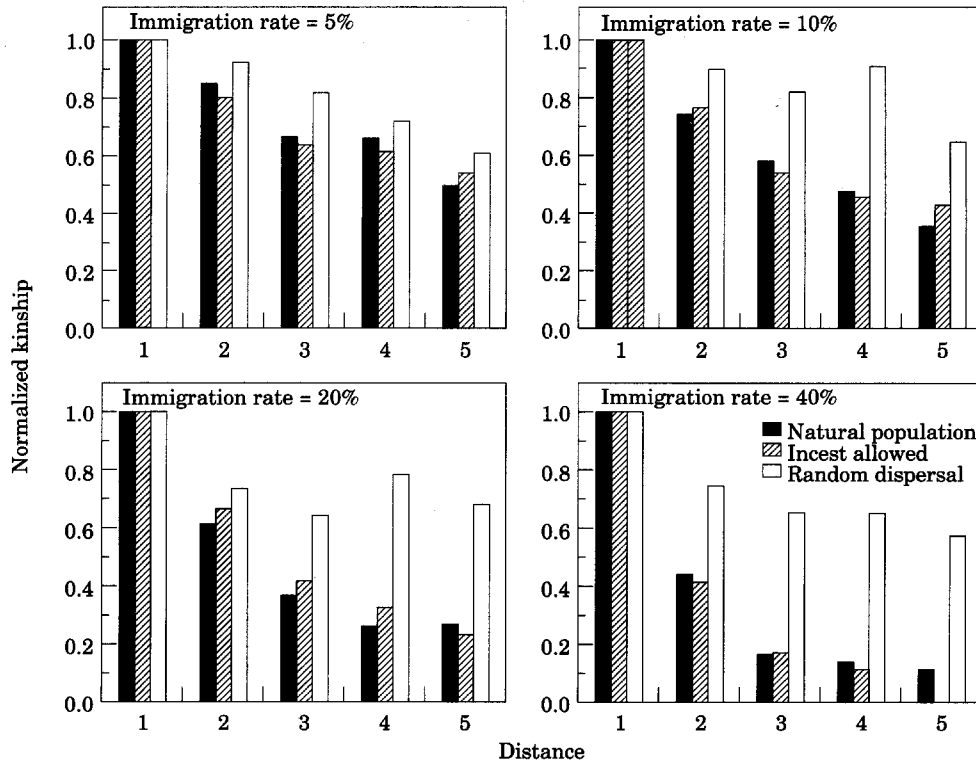


FIG. 3. Coefficients of kinship between oldest auxiliary females and potential mates in groups successively farther from the female's territory (overall mean coefficients of kinship for the last 50 annual cycles of the simulations normalized each year to the coefficient of kinship between oldest auxiliary females and males one territory away).

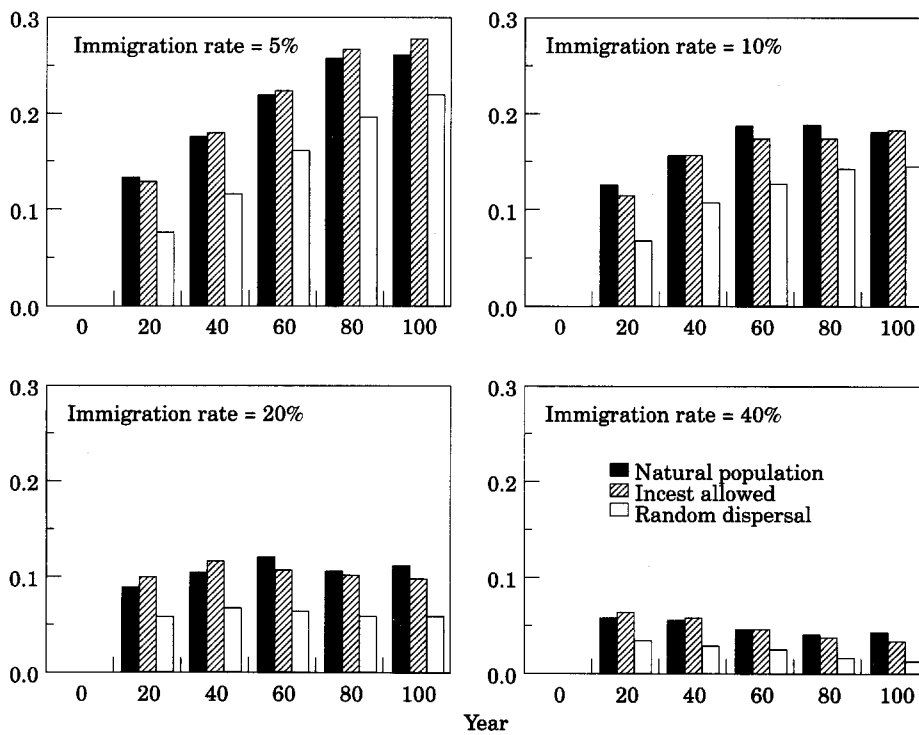


FIG. 4. Overall mean coefficients of kinship between oldest auxiliary females and males in adjacent territories during the course of 100 annual cycles in simulated populations. See Fig. 1 for further explanation.

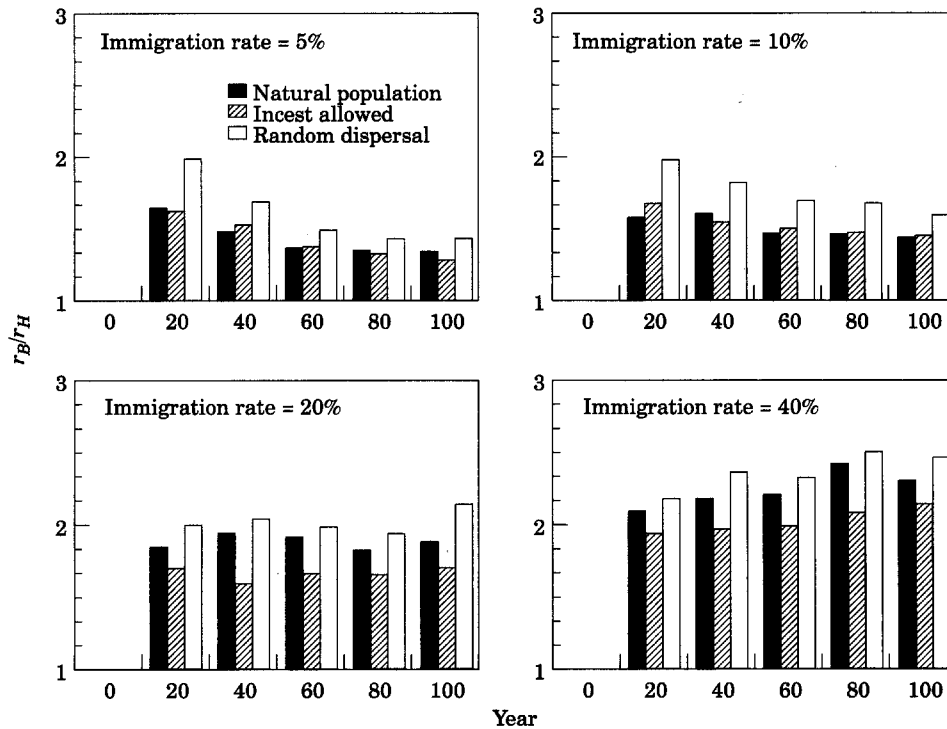


FIG. 5. Critical relatedness ratios (r_B/r_H) for helping by oldest auxiliary females during the course of 100 annual cycles in simulated populations. r_B , the oldest auxiliary females' relatedness to the young they could raise if they mated with males in adjacent territories; r_H , their relatedness to the young they could help to raise in their natal groups. Note that the ordinate begins at 1.0, the theoretical minimum for the relatedness ratio.

thus the critical value of G/L never reached 2.0—the expected value for a large, randomly breeding population in which oldest female auxiliaries raised young that were on average half siblings. The simulations showed that under these social conditions only the highest level of immigration (40%) resulted in relatedness ratios exceeding 2.0.

Restricted dispersal and low immigration tended to increase both coefficients of kinship for oldest auxiliary females, f_{Bi} and f_{Hi} , by increasing the relatedness of mates and consequently the relatedness within groups in general. The changes, however, were consistently greater for f_{Hi} than for f_{Bi} . As a consequence, $r_B/r_H (=f_{Bi}/f_{Hi})$ decreased. Thus both restricted dispersal and partial isolation of populations relaxed the conditions for the evolution of helping by kin selection.

5. Discussion

5.1. COMPARISON OF MODEL AND NATURAL POPULATIONS

Our simulations have allowed us to identify some long-term genetic consequences of a complex social system. Pedigrees can rarely provide this information, because even decades of study are insufficient to

establish adequate genealogies. Although the pedigrees available for stripe-backed wrens suggest that mates are seldom related (Rabenold, 1985), the longer perspective provided by our simulations suggests that mates are indeed often genealogically related.

DNA fingerprinting of stripe-backed wrens has revealed two features of social behavior not incorporated into the simulation. Evidence now suggests that the oldest male helper sires about 0.17 of all offspring in groups in which the breeding female is no longer the helper's mother or about 0.10 of offspring overall (Stevens, 1988; Rabenold *et al.*, 1991a; Piper & Slater, 1993). This behavior has consequences for the advantages to males of remaining in auxiliary positions but might not have significant consequences for the genetic structure of the population or for advantages of helping. The oldest male helper is usually a brother or son of the breeding male and a brother of the oldest female helper. Thus this male's participation in reproduction would have little effect on the expected relatedness of mates or of an older female helper to the young she raises.

In addition, recent evidence shows that some pairs without helpers are joined by unrelated juvenile males immigrating from a distance (Piper *et al.*, 1995). These unrelated male auxiliaries can participate in reproduc-

tion in these small groups or succeed to a breeding position if the principal male dies. Apparently about 16% of juvenile males disperse in this way and at least half of those eventually reproduce in their new populations, mostly in small groups with lower than average reproductive success. Immigration by unrelated females into groups with average or above average reproductive success, as incorporated in the simulations, occurs more frequently. Both forms of immigration into stripe-backed wren populations probably do not together exceed 15–20% of breeding vacancies. Further work with this model could explore the influence of these refinements of social dynamics.

To compare the levels of inbreeding in the simulated populations with direct measurements on natural populations, we need to isolate the proportion of the inbreeding coefficient attributed to non-random mating. Our simulations allowed us to use a simpler procedure to partition inbreeding coefficients than that employed in more formal analysis (Crow & Kimura, 1970: 104–108). First, to correct for the small contribution of incest to inbreeding in the RD condition, we added to the inbreeding coefficients for the RD condition the difference between those for the IA and NP conditions. Then we divided the corrected values for the RD condition by those for the NP condition to obtain the proportion of the inbreeding coefficient contributed by non-random mating. The remainder was contributed by the partial isolation of the simulated populations.

When inbreeding was partitioned in this way into components of isolation and non-random mating, the partial isolation of populations on average accounted for 85% of the inbreeding coefficient after 100 annual cycles with a 10% rate of immigration, and 69% with a 20% rate of immigration. Thus, for immigration rates approximating those in the natural population (10 to 20%), non-random mating contributed 15 to 30% of the inbreeding coefficient.

This estimate falls within the range of inbreeding coefficients measured by heterozygote deficits in electrophoretic data from a natural population of stripe-backed wrens (4 to 22%; Stevens, 1988). While both of these estimates measure relatedness in excess of that expected under random mating, the estimates from heterozygote deficits do not indicate identity by descent.

Another indication of inbreeding in populations of stripe-backed wrens is the marked difference between nearby populations in the frequencies of matriline-specific restriction fragments in nuclear DNA (Rabenold *et al.*, 1991b). At least in one stable population, the high frequency of one such fragment confirms that most breeding females are recruited from

within the population.

Genetic studies of other cooperatively breeding species have failed to find evidence of inbreeding (Johnson & Brown, 1980; Mumme *et al.*, 1985; Vehrencamp *et al.*, 1986; Wrege & Emlen, 1987). The absence of significant inbreeding in the gray-crowned babbler (*Pomatostomus temporalis*) is especially noteworthy because the babbler's social behavior (Brown, 1987) resembles that of the stripe-backed wren.

Observations of matings also suggest that inbreeding levels are low for other cooperatively breeding species. However, reports on these species have yet to include the long-term consequences of demographic and social features for genetic structure. For instance, although close incest is rare among Florida scrub jays (*Aphelocoma coerulescens*) (Woolfenden & Fitzpatrick, 1984), its demographic and social characteristics suggest genetically structured populations. Our simulations have shown that behavioral mechanisms for avoiding close incest do not preclude significant inbreeding.

5.2. DETERMINANTS OF GENETIC STRUCTURE

Relatedness within groups was determined by the turnover of breeders and the level of inbreeding in the population. In our simulations, inbreeding increased relatedness within groups above the levels expected from short pedigrees. Thus, although oldest auxiliary females in these simulations usually helped to raise half sibs, just as in natural populations (Rabenold, 1985, 1990), their coefficients of kinship to these young were considerably higher than expected for a large, randomly mating population.

Relatedness between members of different groups depended on the distance between the groups. This correlation of spatial and genetic distances between groups, although influenced by immigration rate, resulted from restrictions on dispersal. The few individuals who moved in any one season usually moved no farther than a neighboring group.

Close incest tended to increase relatedness between mates in the simulations, as expected. However, because incestuous matings occurred infrequently, their effects on inbreeding were small in comparison to those of restricted dispersal and immigration.

Although immigration strongly influenced the genetic structure of the simulated populations, the influence was less than expected from isolation-by-distance models (Wright, 1946; Kimura & Weiss, 1964). Immigration not only introduced new alleles into the simulated populations but also tended to maintain a larger number of successfully breeding groups and thus

a larger effective population size, both conditions that tended to reduce genetic structure in populations (Wright, 1969, 1978; Cavalli-Sforza & Bodmer, 1971). Nevertheless, both inbreeding level and genetic correlation with distance remained significant even when 40% of breeding positions for females were filled by immigrants. Since the highest immigration rates used in the simulations were well above the rate (10–20%) for a natural population of these wrens, it seems unlikely that immigration in natural populations would preclude the development of genetic structure.

5.3. KIN SELECTION IN GENETICALLY STRUCTURED POPULATIONS

The increase in relatedness and inbreeding in any finite population as a result of random losses of alleles does not in itself contribute to the evolution of helping by kin selection (Grafen, 1984). Kin selection requires that the frequencies of an allele for altruism must be higher in actors and recipients than the frequency of the allele in the population (Grafen, 1985; Queller & Goodnight, 1989). This condition is met when help is directed toward individuals more closely related to the actor than randomly chosen recipients (Queller, 1994). Hamilton's rule for the evolution of helping by kin selection applies to finite populations only if relatedness is adjusted for the level of inbreeding in the population. In comparing individuals' behavioral alternatives, we have used ratios of relatedness in which these adjustments cancel. Relatedness ratios thus allow us to compare the possibilities for kin selection under social conditions that differ in overall levels of inbreeding.

Kin selection in our simulations always favored helping by females in groups of four. Based on the productivity of groups of different sizes in the natural population, it was advantageous for individuals to remain as the second helper in a group rather than to disperse when their relatedness to the young they raised was more than about 29% ($1/3.43$) of their relatedness to young they could produce on their own. Genetic structure in the simulated populations kept these ratios well above 29% for helpers in groups of four, even for the oldest auxiliary females. The simulations thus confirm that kin selection can provide a sufficient explanation for one feature of the Saman population of stripe-backed wrens.

A complete explanation for the evolution of cooperative breeding in a species like the stripe-backed wren will require examination of (1) the advantages of helping as opposed to dispersing for other helpers in a group and (2) the conditions for the original spread of this behavior in a population as well as its

maintenance. Such analyses might include a combination of direct benefits of delayed dispersal and helping, both immediate and delayed (Wiley & Rabenold, 1984), as well as indirect benefits of helping to rear kin. Full understanding of the evolution of cooperative breeding in this species will also require knowledge of the variation in demographic parameters among populations and the ecological conditions that permit auxiliaries to increase the productivity of their natal groups (Brown *et al.*, 1981; Emlen, 1982; Stacey & Ligon, 1987).

5.4. EVOLUTIONARY INTERACTION OF SOCIAL AND GENETIC STRUCTURE

The lessons from our simulations also pertain to two wider evolutionary issues: possibilities for group selection and for rapid evolution through positive feedback. Selection at the level of groups of individuals has remained controversial, despite several theoretical treatments (Levin & Kilmer, 1974; Wilson, 1977, 1983; Uyenoyama & Feldman, 1980; Michod, 1982), because it remains uncertain whether the population structure required by these models occurs in nature (Wade & Bredon, 1987; Chepko-Sade *et al.*, 1987). Most natural populations have higher immigration rates and larger population sizes than are consistent with these models (Templeton, 1987). Our simulations, however, show that significant genetic structure can result from social behavior even when immigration rates are high.

The long-term perspective provided by our simulations also suggests that the genetic and social structures of populations might evolve in concert. In the case analyzed here, short-range dispersal generates conditions that favor the evolution of helping and a concomitant delay in dispersal. The crucial ecological constraint on the evolution of helping by kin selection is the marginal gain in a group's reproductive success as a result of the presence of helpers. By altering the genetic relatedness of individuals to their genealogical relatives, short-range dispersal reduces the marginal gain sufficient for the evolution of helping and delayed dispersal.

The converse also holds: delayed dispersal produces conditions that favor the evolution of short-range dispersal. Among stripe-backed wrens, the disappearance of a breeding female from a large group triggers intense competition among dispersing females to fill the vacancy. It is the oldest female auxiliaries from nearby territories, those that have delayed dispersal, that compete most effectively for these vacancies (Zack & Rabenold, 1989; Zack, 1990). If nearby females have an advantage over distant rivals, then delayed dispersal creates conditions that favor short-range dispersal.

These reciprocal consequences of short-range dispersal and delayed dispersal are mutually reinforcing and thus could produce "runaway social evolution" (Wade & Bredon, 1987). Once started in this direction, evolution might quickly lead to socially complex and genetically viscous populations.

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