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The effects of dispersal behaviour in group selection

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ABSTRACT

Individual-based simulations were conducted to examine the spread of an altruistic allele by group selection. For the simulations, individuals with one locus determining altruistic behaviour were created in an environment with 13 patches. Individual fitness was determined by the number of altruists and the number of total individuals in a patch. Offspring disperse within the natal patch or into neighbouring patches depending on random values with a normal distribution having a zero mean and standard deviation σ_d (random dispersal model). The probability of the spread of the altruistic allele increased with increasing dispersal distance until a moderately low dispersal distance ($\sigma_d = 50$); thereafter, the probability decreased with increasing dispersal distance. A density-dependent dispersal model in which female offspring tend to disperse to the patch with lowest densities among five candidate dispersal sites was also tested. For the density-dependent dispersal model, the chance of spreading the altruistic allele was higher than that of the random dispersal model. The results can be explained by two components of group selection: the extinction of groups with lower frequencies of altruists (selective extinction) and higher frequencies of migrants of altruists due to high productivities of altruistic groups (effective migrants). Evolution of altruism by interdemic group selection only (i.e. by differential extinctions and recolonization of demes) appears unlikely, since it requires high rates of both extinction and recolonization with low migration among surviving demes. However, the present study showed that moderately low migration can create favourable conditions under which both selective extinction and effective migrants simultaneously increase the probability of spreading the altruistic alleles.

Keywords: altruistic behaviour, dispersal, individual-based model, interdemic group selection, intrademic group selection.

INTRODUCTION

The importance of group selection as an evolutionary process has been much debated (Maynard Smith, 1964, 1983; Williams, 1966; Lewontin, 1970; Wade, 1978; Wilson, 1983; Grafen, 1984). Group selection can be classified into two categories: interdemic and intrademic group selection (Wade, 1978; Wilson, 1983). Interdemic group selection can occur where a population is subdivided into demes among which there is complete or partial isolation. Allele frequencies in the population will change by the differential extinction and

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recolonization of these partially isolated local demes. Intrademic group selection assumes that individuals belong to different groups (trait groups) at one stage of their lifetime, and that they disperse after reproduction. Changes in allele frequencies will be caused by mixing individuals in a global population after the differential reproduction of the groups. Intrademic group selection has been considered to be a more common process than interdemic group selection (Wilson, 1977, 1983; Wade, 1978).

Both types of group selection require significant variation among groups. When the variation among groups is caused by limited dispersal of offspring, so that related individuals interact with each other, the process acting among the groups is called 'kin selection'. In fact, Wilson (1977) and Wade (1978) regarded kin selection as a special case of intrademic group selection. Wade (1980, 1985) showed that the models of kin selection and group selection can be represented as variations of a common general model. If kin groups are partially isolated and subject to extinction, kin selection can also be regarded as interdemic group selection.

Limited dispersal causes a population structure that promotes interaction among relatives. This structure has been called 'population viscosity'. Population viscosity often facilitates the evolution of altruism by increasing the degree of relatedness among interacting individuals. However, if local groups are regulated by a carrying capacity after the expression of altruism but before the formation of new groups, then the effects of differential productivity of groups are eliminated and altruism cannot evolve. Wilson *et al.* (1992) showed by simulation that population viscosity with local regulation cannot promote kin selection or intrademic group selection. The same results hold in mathematical models of a patch-structured population (Taylor, 1992a; Bulmer, 1994).

Many models of interdemic group selection have concluded that an important factor promoting group selection is low or no migration among groups. Low migration promotes phenotype and genotype variation among groups and causes high extinction rates. Aoki (1982) modelled interdemic group selection and found that such selection becomes more effective with decreased migration rates when the selection coefficients of groups and individuals are constant. Kimura (1983) reached the same conclusion by using diffusion models. When the migration rate is constant, the turnover rates of the groups are an important factor promoting interdemic group selection (Aviles, 1993). However, ongoing local extinction implies ongoing recolonization, which constitutes gene flow, and gene flow will reduce genetic variation among groups (Slatkin, 1985; Harrison and Hastings, 1996). Thus, several authors (Maynard Smith, 1976; Slatkin, 1985; Harrison and Hastings, 1996) have suggested that interdemic group selection is unlikely because low gene flow or migration is required for divergence among groups and for high extinction rates, but this simultaneously reduces the chances of recolonization and the spread of group-selected alleles.

Dispersal behaviour simultaneously affects many factors, including genetic variations among groups, extinction rates, recolonization rates, local population regulation and alleles dispersing to a global population. These factors have different influences on the effectiveness of group selection. Mathematical models have assumed that these factors are independent parameters and are often *a priori* assumed relationships among different parameters. However, these are interconnected phenomena that have emerged through interactions among many factors. Furthermore, not only dispersal distance of individuals, but also the types of behaviour – such as density-dependent dispersal – may affect the outcomes of group selection. Differential extinction and recolonization, differential productivity of groups, and differential dispersal rates of genotypes have been recognized as processes promoting group selection. However, the relative importance of simultaneously operating these processes has not been examined.

I conducted individual-based simulations that assume only reproduction and dispersal behaviour of individuals. In these individual-based simulations, population level phenomena, such as extinction, population size, genetic variation among groups and new group formation, emerge as the consequences of individual reproduction and dispersal. The aims of this study were two-fold: (1) to examine the effect of dispersal distance and types of dispersal behaviour (random dispersal and density-dependent dispersal) on evolution of altruism by group selection, and (2) to determine the relative importance of differential extinction and recolonization and differential dispersal rates of genotypes in the evolution of altruism.

METHODS

The model

To explore the evolution of altruism in subdivided populations, I constructed an individual-based simulation model with the following features:

1. *General life history of simulated organisms.* Individuals live only in patches in which they interact, mate and reproduce. Each individual has data for location (x-y coordinates), sex and a locus with two alleles that affect altruistic behaviour. Altruistic behaviour can occur only in females. Females reproduce sexually and their fitness is based on their genotypes and the composition and the number of individuals in the patch. The offspring disperse from their birth sites. After offspring dispersal, all adult individuals die.
2. *Habitat.* A two-dimensional landscape consists of 13 patches in which organisms can live (Fig. 1). The patches are 40 × 40 squares arranged in a checkerboard pattern. The distance to the nearest patches is 56.57 (equal to the diagonal of a patch).
3. *Fitness.* The fitnesses of each of the female genotypes are:

$$W_{AA} = 2 - c + nb + r(1 - N/K) + v$$

$$W_{Aa} = 2 - 0.5c + nb + r(1 - N/K) + v$$

$$W_{aa} = 2 + nb + r(1 - N/K) + v$$

where b is the benefit of altruism to the recipient; c is the cost to the actor; r is the coefficient of density dependence; K is the carrying capacity of a patch in which all individuals do not incur cost and do not receive benefit (i.e. all individuals are non-altruists; hereafter, a carrying capacity of a patch = K); N is the number of individuals with which an individual interacts in the patch; n is the number of altruists with which an individual interacts in the patch. The number of altruists is calculated as (the number of individuals with genotype AA in the patch) + 0.5 (the number of individuals with genotype Aa in the patch). This function assumes that a single altruist increases the fitness of every individual in its interaction neighbourhood (including itself) by an amount of b for genotype AA or by an amount $0.5b$ for genotype Aa. Finally, v is a random factor that is a random number from a normal distribution with zero mean and 0.1 standard deviation. Because the values of

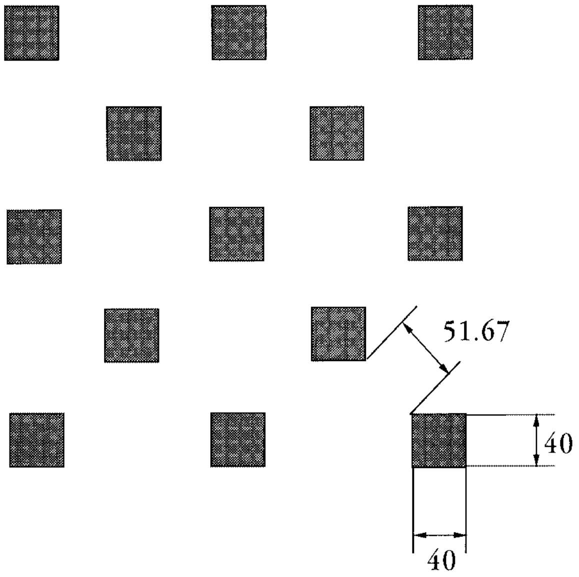

Fig. 1. Simulation area containing 13 patches.

these fitnesses are real numbers, the number of offspring that a female gives birth to is calculated by:

$$\text{number of offspring} = \text{round(fitness)}$$

where round(x) is x-rounded to the nearest integer. There are two reasons for the addition of v to the fitness formula. First, by adding random noise, the effect of the round-off will be reduced. For instance, when fitness values of two females are calculated as 1.6 and 1.7, both females are set to give birth to two offspring. By adding random noise, the average number of offspring produced by many females with fitness values of 1.6 will be smaller than that produced by females with fitness values of 1.7. Second, a random factor will cause stochastic extinction. By adding stochastic factors, patches with smaller numbers of individuals will be more likely to become extinct.

4. *Reproduction.* Females randomly choose a male as a mate within the patches and reproduce based on fitness. For the offspring's locus, one allele was randomly chosen from the mother and the other was randomly chosen from its mate.

5. *Dispersal.* The offspring dispersal site was determined in two ways:

- *Random dispersal model.* The dispersal distance (d) was a random value with a normal distribution with a zero mean and standard deviation σ_d. If the random value was negative, the value was converted to positive. The direction of dispersal was a random angle ranging from 0 to 2π. Thus, the x and y coordinates of a dispersal site were x[mother] + cos(angle)*d and y[mother] + sin(angle)*d, respectively. A candidate dispersal site was accepted if it was within the patch (either the natal patch or a non-natal patch). This means that individuals can disperse only to patches. If a candidate dispersal site was located outside the patch, a new candidate dispersal site was generated. This algorithm of dispersal behaviour results in the correlation between the standard deviation σ_d of dispersal distance and migration rates among patches. After offspring dispersal, all adult individuals were removed.

- *Density-dependent dispersal model.* The dispersal algorithm is that used by Kawata (1995). Five acceptable dispersal sites were determined for each offspring by the same method used in the random dispersal model. The number of offspring within the patch was counted for each of the five sites. Offspring choose the site with the lowest density of offspring. This procedure means that individuals disperse to the patch with the lowest density among randomly chosen sites. After offspring dispersal, all adult individuals were removed.

The program was written in CodeWarrior C++ for the Power Macintosh.

Measurements

Gene frequency

To examine the conditions for evolving an altruistic allele, each simulation with different parameter settings was conducted for 500 generations, and the gene frequencies of the altruistic allele in a global population at the 500th generation were measured. One hundred replicates with the same parameter settings were conducted and the average gene frequencies were calculated.

Indices for population viscosity and variation in patch size among populations

To measure the variation in genotype frequency among patches, I used the population viscosity index (Wilson *et al.*, 1992). The gene frequency change under different genotype fitnesses is:

$$\Delta p = \frac{pq[p(\bar{W}_{AA} - \bar{W}_{Aa}) + q(\bar{W}_{Aa} - \bar{W}_{aa})]}{\bar{W}}$$

where p and q are the gene frequencies of the altruistic allele, A, and the non-altruistic allele a, respectively. $\bar{W}_{AA}$, $\bar{W}_{Aa}$ and $\bar{W}_{aa}$ are the average fitnesses of female genotypes AA, Aa and aa, respectively. $\bar{W}$ is the average fitness of all individuals.

$\bar{W}_{AA}$, $\bar{W}_{Aa}$ and $\bar{W}_{aa}$ were calculated as:

$$\begin{aligned} \bar{W}_{AA} &= 2 - c + \bar{n}_{AA}b + r(1 - \bar{N}_{AA}/K) + v \\ \bar{W}_{Aa} &= 2 - 0.5c + \bar{n}_{Aa}b + r(1 - \bar{N}_{Aa}/K) + v \\ \bar{W}_{aa} &= 2 + \bar{n}_{aa}b + r(1 - \bar{N}_{aa}/K) + v \end{aligned} \tag{1}$$

where $\bar{n}_{AA}$, $\bar{n}_{Aa}$ and $\bar{n}_{aa}$ are the average numbers of altruists with which genotypes AA, Aa and aa interact in the patch, respectively (the average over all individuals of each genotype). $\bar{N}_{AA}$, $\bar{N}_{Aa}$ and $\bar{N}_{aa}$ are the average numbers of individuals with which genotypes AA, Aa and aa interact in the patch, respectively.

The condition for $\Delta p > 0$ is:

$$p(\bar{W}_{AA} - \bar{W}_{Aa}) + q(\bar{W}_{Aa} - \bar{W}_{aa}) > 0$$

$\bar{W}_{\mathrm{AA}}$, $\bar{W}_{\mathrm{Aa}}$ and $\bar{W}_{\mathrm{aa}}$ are replaced by formulae (1). Then,

$$b[p(\bar{n}_{\mathrm{AA}} - \bar{n}_{\mathrm{Aa}}) + q(\bar{n}_{\mathrm{Aa}} - \bar{n}_{\mathrm{aa}})] + [pr(\bar{N}_{\mathrm{Aa}} - \bar{N}_{\mathrm{AA}})/K + qr(\bar{N}_{\mathrm{aa}} - \bar{N}_{\mathrm{Aa}})/K] - 0.5c > 0 \qquad (2)$$

Formula (2) becomes $V > (c - D)/b$ when:

$$V = 2[p(\bar{n}_{\mathrm{AA}} - \bar{n}_{\mathrm{Aa}}) + q(\bar{n}_{\mathrm{Aa}} - \bar{n}_{\mathrm{aa}})] \text{ and}$$

$$D = 2(pr(\bar{N}_{\mathrm{Aa}} - \bar{N}_{\mathrm{AA}})/K + qr(\bar{N}_{\mathrm{aa}} - \bar{N}_{\mathrm{Aa}})/K)$$

The term V is similar to the population viscosity index and the coefficient of relationship (r) in Hamilton's rule (Wilson *et al.*, 1992). D represents the variation in population size among patches.

The probability of spreading altruistic alleles will increase when individuals of genotype AA (or Aa) interact with a larger number of altruists than those of genotype Aa (or aa) in the patches. Simultaneously, the probability of spreading altruistic alleles will decrease when individuals of genotype AA (or Aa) interact with a larger number of individuals than those of genotype Aa (or aa) in the patches. When the population size is equal among the patches, $D = 0$ and the condition for increasing the altruistic allele is $V > c/b$. When individuals randomly interact and the number of altruists is equal among the patches, $V = 1$ and the condition for increasing the altruistic allele is $b > c$. V becomes 1 in a randomly interacting global population, since an altruist receives benefit from itself, so that $\bar{n}_{\mathrm{AA}}$ and $\bar{n}_{\mathrm{Aa}}$ are larger than $\bar{n}_{\mathrm{aa}}$ by 1 and 0.5, respectively. The condition for increasing the altruistic allele, $V > (c - D)/b$, does not consider complicated factors such as extinction–recolonization and migration rates, so that if an altruistic allele evolves when $V \leq (c - D)/b$, some of these factors can affect the frequencies of the altruistic allele.

V and D were measured for different values of σ_d. The average values of V and D were measured over 100 generations and over the same genotypes. The values were calculated only when the average gene frequencies over 100 generations were in the range 0.45–0.55, since V and D change dependent on gene frequencies and it is difficult to manipulate gene frequencies.

Extinction rates and recolonization

The numbers of extinctions and recolonizations were counted over 500 generations. The initial gene frequency of the altruistic allele was set at 0.5. The average values over 10 simulation runs were used. One extinction was counted when the population size in a patch became zero. One recolonization was counted when the population size in a patch recovered from zero and remained >2 for more than five generations.

The average length of population persistence was taken as the average number of generations until a population became extinct in a patch. The initial conditions for the population were set at gene frequency = 0 and no migration. The average length of population persistence over 10 simulation runs was used.

To ensure that extinctions cause changes in gene frequencies, extinct populations should have gene frequencies that are significantly different from the average gene frequencies of a global population. Thus, gene frequencies of extinct populations were measured in the second generation before the extinctions. The average frequencies over 100 extinctions were measured. If the gene frequencies of a global population are high or low, the gene frequencies of extinct populations will also be high or low. Thus, the gene frequencies of extinct populations were measured only when gene frequencies of the global population ranged from 0.4 to 0.6. The gene frequencies of extinct populations were not measured for $\sigma_d = 100$, 150 and 200, since at these values of σ_d there were no or few extinctions.

Migration rates and the number of effective migrants

Migration rates were measured by counting the number of offspring that disperse to patches that were not the natal patch. Then, the average number of migrants per patch per generation was calculated.

If the number of altruists which disperse into patches with lower frequencies of altruists are larger than those of non-altruists which disperse into patches with higher frequencies of altruists, the altruistic alleles will increase. Thus, the number of migrants whose frequencies of altruistic alleles were larger (M_a) and smaller (M_n) than those of the groups in patches to which they migrated were counted. Then, the differences between M_a and M_n ($M_a - M_n$) were calculated for each generation. When $M_a - M_n$ is positive, the altruistic alleles are likely to increase. Thus, I call $M_a - M_n$ 'the number of effective migrants'. The numbers of effective migrants were summed until the 100th generation, and averaged over 100 replicates.

Simulation runs

For all simulations, the initial number of individuals was set to 200 and the initial gene frequencies at the altruistic locus were set to 0.5; b was set to 0.05. For most of the simulations, the random factor (v) was 0.1 and the reproductive rate (r) was 1.5. The simulations of the random dispersal model were conducted by varying (1) σ_d, the standard deviation of the dispersal distance of both female and male offspring ($\sigma_d = 20$, 40, 50, 75, 100, 150 and 200); (2) the cost ($c = 0$, 0.025, 0.05, 0.075, 0.1, 0.0125, 0.015 and 0.2); and (3) the carrying capacity in a patch ($K = 16$, 20, 24). To examine the effect of reproductive rate and random factors, r and v were varied ($r = 0.125$, 0.15, 0.175, 0.2 and 0.225; $v = 0.05$, 0.1, 0.15, 0.2, 0.25 and 0.3) keeping $\sigma_d = 50$, $c = b = 0.05$ and $K = 20$. The simulations were iterated over 100 times with the same parameters. The simulations of the density-dependent dispersal model were conducted by varying σ_d ($\sigma_d = 20$, 40, 50, 75, 100, 150 and 200) keeping $K = 20$, $r = 0.15$ and $v = 0.1$. The following results refer to the random dispersal model unless otherwise stated.

RESULTS

Migration rates

Figure 2 shows the average number of emigrants per patch per generation; that is, the number of offspring that dispersed from the natal patch to another patch. When $\sigma_d = 20$, there were no migrants among patches. The migration rates increased with dispersal distance. The number of migrants per patch increased with increasing carrying capacity of a patch, K. For the density-dependent dispersal model, the number of migrants was larger than for the random dispersal model.

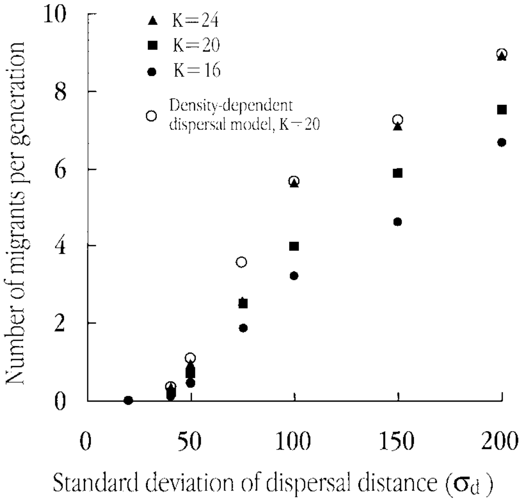

Fig. 2. Number of migrants from the natal group to other groups per generation. Parameter values: $v = 0.1$, $r = 1.5$, $b = c = 0.05$.

Extinction and recolonization

The average numbers of extinctions and recolonizations during 500 generations are shown in Fig. 3. When the carrying capacity of a patch (K) was set to 16 and 20, the numbers of extinctions and recolonizations were largest when dispersal distance was moderately low ($\sigma_d = 50$). The number of extinctions and recolonizations decreased when $\sigma_d > 50$. For $K = 24$, the number of extinctions decreased with increasing dispersal distance (from $\sigma_d = 20$ to 100). For all values of K, there were no recolonizations when $\sigma_d = 20$. There were no extinctions or recolonizations when dispersal distances were large ($\sigma_d = 100$ for $K = 24$ and $\sigma_d = 150$ for $K = 20$ and 24). The numbers of extinctions decreased with increasing K. For the density-dependent dispersal model, the numbers of extinctions and recolonizations were smaller than those for the random dispersal model.

Figure 4 shows the average number of generations of population persistence when there was no migration. A population in a patch could persist longer when K was larger. The difference in the number of generations of patch persistence between the populations of all altruists (gene frequency $= 1$) and all non-altruists (gene frequency $= 0$) was largest when $K = 20$ and smallest when $K = 24$.

The number of individuals in a patch

Figure 5 shows the average number of individuals that interacted with each genotype in a patch. The values were measured during the first 100 generations and the average gene frequency of altruistic alleles ranged from 0.45 to 0.55. The number of individuals that interacted with genotype AA was larger than the number of individuals that interacted with genotypes Aa and aa from $\sigma_d = 20$ to 150. The difference in the number of individuals between genotypes decreased with increasing σ_d. There was almost no difference in the

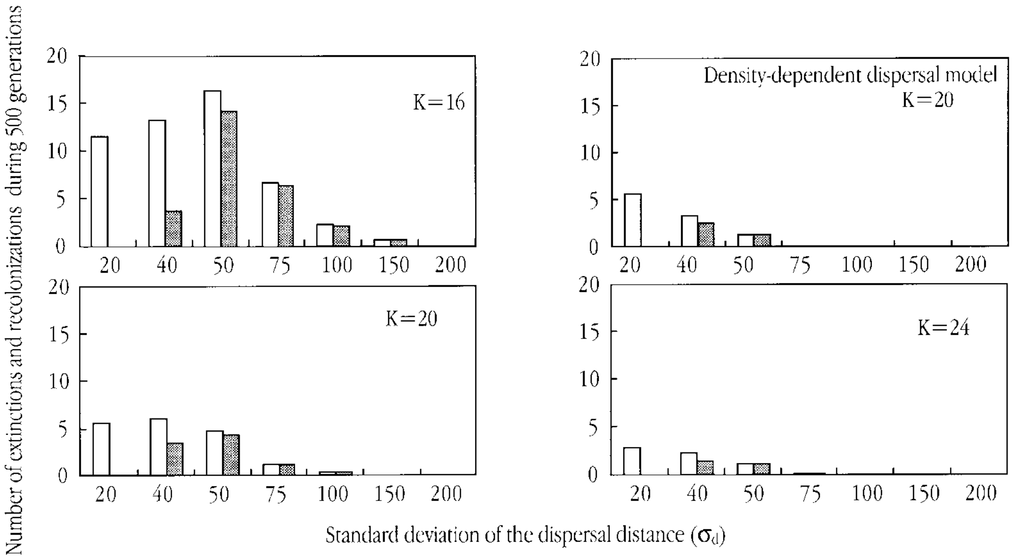

Fig. 3. The numbers of extinctions and recolonizations during 500 generations. Parameter values: $v = 0.1$, $r = 1.5$, $b = c = 0.05$. □, extinctions; ■, recolonizations.

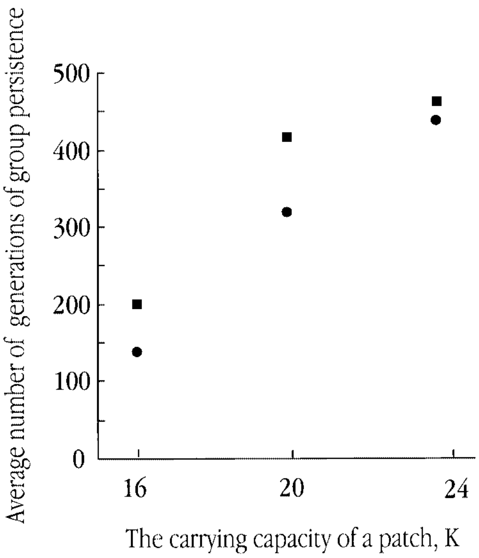

Fig. 4. Average number of generations of group persistence. Average persistence was measured as the number of generations until a population became extinct in a patch. Parameter values: $v = 0.1$, $r = 1.5$, $b = c = 0.05$. ■, all altruists; ●, all non-altruists.

number of individuals among genotypes when $\sigma_d = 200$. For the density-dependent dispersal model, the number of individuals in a patch was almost the same as that in the random dispersal model.

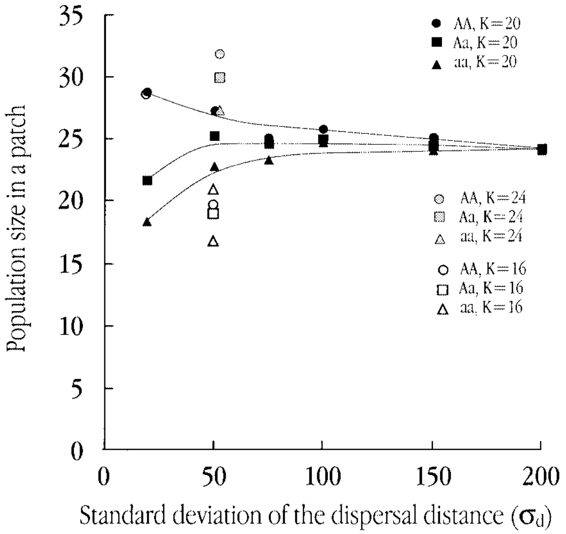

Fig. 5. The average number of individuals that interact with a particular genotype in a group. Parameter values: $v = 0.1$, $r = 1.5$, $b = c = 0.05$.

Population viscosity

The index of population viscosity (V) increased with decreasing σ_d (Fig. 6). V was close to 1 (i.e. random interaction) when the dispersal distance was set at its largest value ($\sigma_d = 200$). V increased with K, but there was little difference in V for different values of K when the dispersal distance was large ($\sigma_d = 150$ and 200). $(c - D)/b$ values mostly corresponded with values of V. For the density-dependent dispersal model, V was smaller than with the random dispersal model. $(c - D)/b$ values were slightly smaller than V values.

Effective migrants and selective extinctions

Figure 7 shows 'the number of effective migrants' (defined in the Methods section) plotted against dispersal distance. The number of effective migrants increased with increasing dispersal distances until $\sigma_d = 50$, and then decreased with larger dispersal distances. When dispersal distance was large ($\sigma_d = 150$ or 200), the number of effective migrants became almost zero. There were few differences in the number of effective migrants for different values of K. For the density-dependent dispersal model, the numbers of effective migrants were greater than with the random dispersal model when $\sigma_d = 40$, 50 and 75.

Figure 8 shows the average gene frequencies of extinct populations. At low to moderate dispersal distances ($\sigma_d < 75$), the gene frequencies of extinct populations were less than 0.5, and thus groups with lower frequencies of altruistic alleles tended to become extinct. The selection difference of groups (i.e. the difference in gene frequencies between extinct populations and surviving populations) increased with decreasing dispersal distance (σ_d).

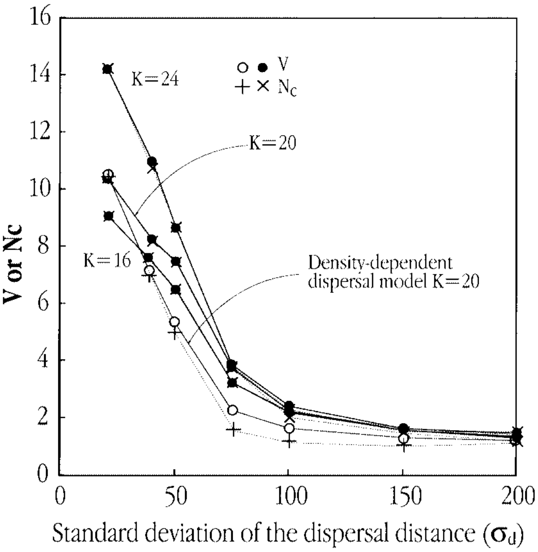

Fig. 6. Population viscosity and variations in the number of individuals among patches. V indicates the population viscosity index. $Nc = (c - D)/b$, where b is the benefit, c is the cost and D is an index of the variation in the number of individuals among patches. Solid line = V, broken line = Nc. If individuals interact randomly within a group population, V becomes 1. Parameter values: $v = 0.1$, $r = 1.5$, $b = c = 0.05$.

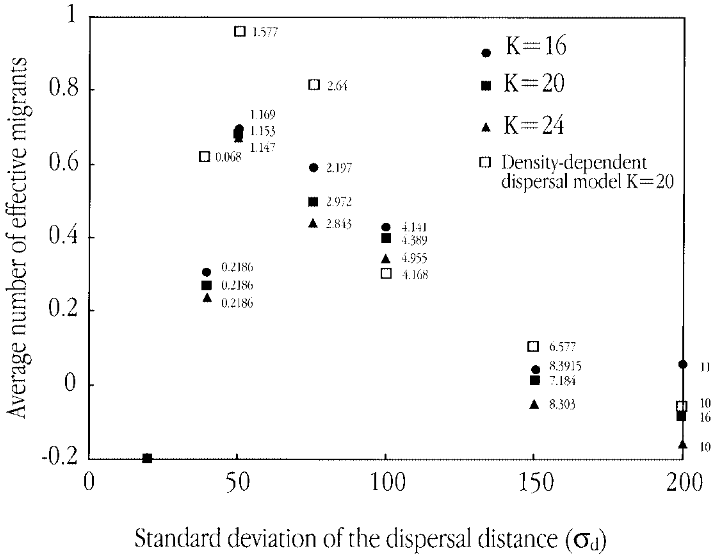

Fig. 7. The number of effective migrants. The number of effective migrants was estimated as the average ($M_a - M_n$) values, where M_a and M_n are the number of migrants whose frequencies of altruistic alleles were larger and smaller, respectively, than those of the groups in patches into which they immigrated. Small numbers to the right of the points indicate the standard error. Parameter values: $v = 0.1$, $r = 1.5$, $b = c = 0.05$.

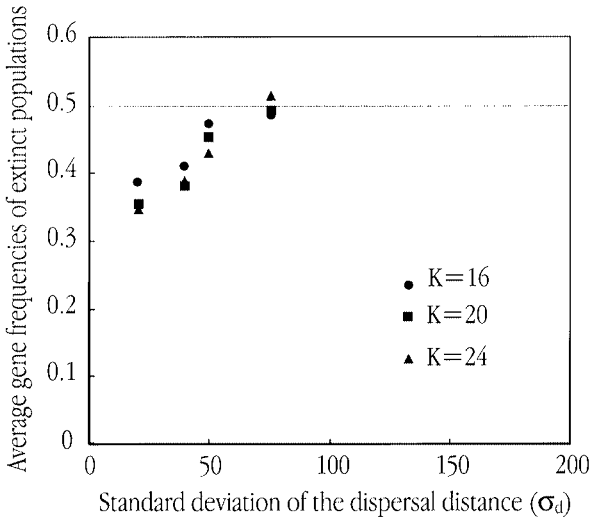

Fig. 8. The average gene frequencies of extinct populations. The gene frequencies were measured in the second generation before extinctions. Parameter values: $v = 0.1$, $r = 1.5$, $b = c = 0.05$.

Gene frequency of the altruistic allele

If cost and benefit are equal ($c = b = 0.05$) and individuals interact randomly, the probability of the spread of altruistic alleles should be 0.5, since V and D become 1 and 0, respectively. For the present simulation, the average frequency of the altruistic allele at the 500th generation for $c = 0.05$ and $b = 0.05$ was about 0.5 when the dispersal distance was set at its largest value ($\sigma_d = 200$) (Fig. 9). The average frequency of the altruistic allele for $c = 0.05$ and $b = 0.05$ was highest when dispersal distance was moderately low ($\sigma_d = 50$) (Fig. 9). The average frequencies decreased when σ_d was raised from 50 to 200. The frequencies increased with increasing K. The frequencies did not change with increasing random factor v (Fig. 10a), but they decreased with increasing reproductive rate r. For the density-dependent dispersal model, the average frequencies of the altruistic alleles were larger than those of the random dispersal model when $\sigma_d = 40$, 50 and 75.

The average gene frequencies of the altruistic allele decreased with increasing cost c ($b = 0.05$, $\sigma_d = 50$ and $K = 20$). When $c = 0.05$, the frequency was larger than 0.5 (Fig. 11). The altruistic allele evolved with a probability larger than 0.5 when $c < 0.07$. For the density-dependent dispersal model, the average gene frequencies of the altruistic alleles were larger than those of the random dispersal model when costs were in the range 0.025–0.15.

DISCUSSION

Limited dispersal is often thought to facilitate the evolution of altruism by increasing the degree of relatedness among interacting individuals. However, Wilson *et al.* (1992) showed that limited dispersal causes a local population regulation that inhibits the evolution of altruism. The effect of increased population viscosity cancels out the effect of local regulation (Taylor, 1992a; Wilson *et al.*, 1992; Bulmer, 1994; but see Kelly, 1992; Queller, 1992).

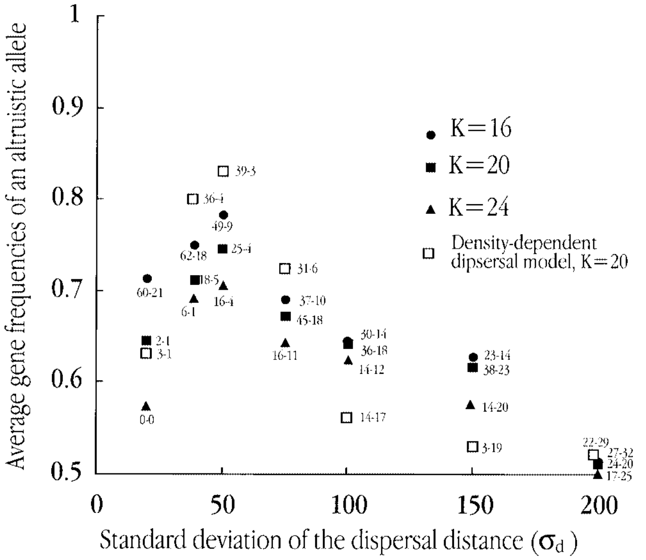

Fig. 9. The average gene frequency of the altruistic allele at the 500th generation over 100 simulation runs. Small numbers below or to the right of the points indicate the number of cases in which the average frequency became 1 (left number) and 0 (right number). Parameter values: $v = 0.1$, $r = 1.5$, $b = c = 0.05$.

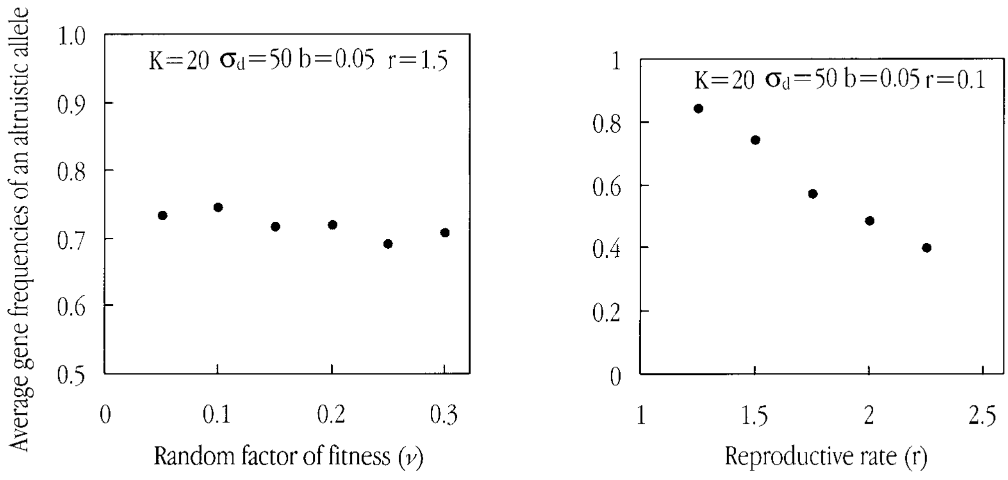

Fig. 10. The average gene frequency of the altruistic allele at the 500th generation over 100 simulation runs. Parameter values: $b = c = 0.05$, $\sigma_d = 50$.

For a randomly interacting population, V and D should = 1 and 0, respectively, and so the condition necessary for an increase in the frequencies of altruistic alleles is $b > c$. Therefore, when $b = c = 0.05$, the probability of spreading the altruistic allele should be 0.5 in a randomly interacting population. In the present simulation, the average gene frequency

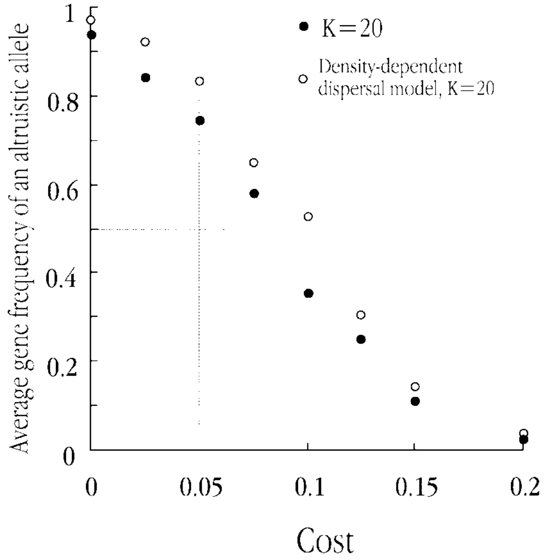

Fig. 11. The average gene frequency of the altruistic allele at the 500th generation over 100 simulations as a function of cost. Parameter values: $\sigma_d = 50$, $v = 0.1$, $r = 1.5$.

of the altruistic allele was 0.5 when $\sigma_d = 200$, but it was larger than 0.5 when $\sigma_d < 200$. For $b = 0.05$ and $\sigma_d = 50$, the average gene frequencies of the altruistic allele were larger than 0.5 when the cost was less than ~0.08. Thus, strong altruism (*sensu* Wilson, 1990) could evolve. As the dispersal distance of offspring decreased, the population viscosity or variation among groups increased (Fig. 6). Individuals in groups with high frequencies of the altruistic allele are given more benefit than those in groups with low frequencies. However, groups with a high frequency of altruists have a larger number of individuals than those with low frequencies of altruists, so that a global population with large values of V simultaneously has larger values of D. The exact values of V and D were difficult to measure, since V and D depend on the number of individuals in a group and on the genetic variation among groups that varies from generation to generation. However, the data in Fig. 6 indicate that V was approximately equal to $(c - D)/b$ (the condition for increasing the altruistic allele is $V > (c - D)/b$). Thus, the effect of increased population viscosity might be cancelled out by the effect of local regulation.

The average frequencies of the altruistic allele were larger than 0.5 when $\sigma_d < 200$, and these were largest when the dispersal distance was moderately low ($\sigma_d = 50$). In addition, when $\sigma_d = 50$, altruistic alleles could spread even if the cost was larger than the benefit ($c < 0.08$ and $b = 0.05$). There are two possible reasons for this: First, groups with high frequencies of altruists have large population sizes and thus a lower probability of extinction than groups with low frequencies of altruists. Interdemic group selection will then increase the frequency of altruistic alleles. Second, groups with high frequencies of altruists have a large population size and thus provide more emigrants to other groups than groups with low frequencies of altruists (here this is called 'effective migration'). This process might be similar to intrademic group selection. I will try to distinguish these two effects in the following discussion.

Figure 12 provides a simple representation of the results shown in Fig. 9. When $\sigma_d = 20$ and $K = 24$, there was almost no migration among groups and only 2–3 groups became extinct. In this case, the average frequencies of the altruistic allele were larger than 0.5 by an amount a, even if there were few extinctions. The reason for this is as follows. Genetic drift might lead to groups that are composed of all altruists or all non-altruists. In this case, the total number of altruists would be larger than the total number of non-altruists because of the larger sizes of the groups with altruists, although there was little or no difference in the number of surviving groups between altruistic and non-altruistic groups. The degree of this effect, a, might decrease with dispersal distance because a difference in the number of individuals between the surviving altruistic and non-altruistic groups would decrease with dispersal distance (Fig. 11).

When there was no migration ($\sigma_d = 20$), the probability of spreading the altruistic alleles differred among $K = 16$, $K = 20$ and $K = 24$. The difference (β and χ) might be due to the effect of selective extinctions. The effects of extinctions are affected by the number of extinctions (Fig. 3) and the selection difference of groups (i.e. the difference in allele frequencies between extinct and surviving groups; Fig. 8). The selection difference did not differ greatly with patch size (K), but the numbers of extinctions for $K = 16$ were larger than those for $K = 20$, which were larger than those for $K = 24$. Therefore, the effects of selective extinctions may only result in an increase in the probability of spreading altruistic alleles with decreasing K.

The numbers of extinctions decreased with increasing dispersal distance (σ_d), although for $K = 16$ and $K = 20$, the number of extinctions increased slightly with decreasing dispersal distance until $\sigma_d = 40$ or 50. The selection difference of groups also decreased

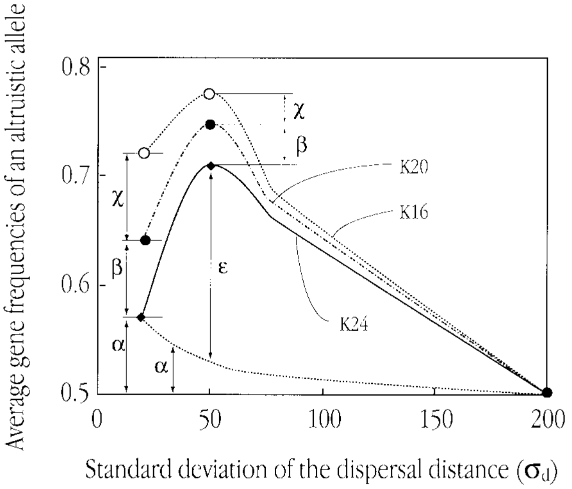

Fig. 12. Simplified representation of the results shown in Fig. 9. a represents the effect of the difference in the number of individuals between altruists and non-altruists without selection. β and χ might be caused by the selective extinction of groups. ε represents the effect of effective migration.

with increasing dispersal distance and, after about $\sigma_d = 75$ or 100, there was no selection difference. Thus, when these two factors are combined (the selection difference of groups and the number of extinctions), the effects of selective extinction might decrease with increasing dispersal distance. In fact, the difference in the probability of spreading altruistic alleles among different values of K (β and χ) decreases with increasing dispersal distance (σ_d).

Although the effects of selective extinctions decreased with increasing dispersal distance, the probability of spreading the altruistic alleles was highest when the dispersal distance was moderately low ($\sigma_d = 50$). The increased probability of spreading the altruistic alleles (ε in Fig. 12) might be due to 'effective migration'. Here, effective migration refers to the case where the gene frequency (altruistic gene) of an immigrant is larger than the average gene frequencies of the groups to which the immigrants disperse. As indicated in Fig. 7, the number of effective migrants was greatest when $\sigma_d = 50$. With increasing dispersal distance, the number of migrants increased but the frequencies of effective migrants decreased when $\sigma_d > 50$, since the difference in gene frequencies among groups decreased and simultaneously the difference in the number of individuals among groups decreased. These effects of migration may cause the patterns of change in the number of effective migrants and ε shown in Fig. 12.

The opposite effect of limited dispersal on group selection (i.e. an increase in genetic variation among groups and a decrease in migration of altruists) has been noted by several authors (e.g. Rogers, 1990; Wilson *et al.*, 1992). In the simulation of Wilson *et al.* (1992), as a result of these two effects, altruism could not evolve in a viscous population. In Rogers' (1990) model, in which altruists were assumed to produce more emigrants (selective emigrants), selective emigrants were facilitated by a high level of migration. The present results show that a moderately low dispersal caused the highest probability of spread of the altruistic alleles. In the present simulations, population size in the patch was allowed to change, so that groups with more altruists had larger population sizes than those with fewer altruists. This may have caused altruists to produce more emigrants than non-altruists, even though, for both altruists and non-altruists, dispersal was randomly determined. Taylor (1992b) showed that altruism can evolve in 'elastic' patches. Here 'elastic' means that the capacity of the patch environment can expand to accommodate extra offspring produced by the altruistic behaviour. The present model allowed patches to have larger numbers of individuals as a result of altruistic behaviour. Thus, the present results conform to Taylor's (1992b) model.

For the density-dependent dispersal model, offspring choose a dispersal site with the lowest number of individuals in the patch among randomly chosen candidate sites. The numbers of individuals in patches with more altruists are larger than the numbers in patches with fewer altruists, so that altruists are more likely to disperse from the patches with more altruists to the patches with less altruists. Thus, the number of effective migrants was larger for the density-dependent dispersal model than for the random dispersal model, and so the altruistic alleles were more likely to spread in the density-dependent dispersal model than in the random dispersal model. For real animals, this type of dispersal behaviour might not be rare (e.g. kangaroo rats; Jones *et al.*, 1985). The density-dependent dispersal might facilitate the evolution of altruism in nature.

Changing the value of the random factor (v) did not affect the results, so that the value ($v = 0.1$) used in the present simulation does not reduce the generality of the model. The average gene frequencies of altruistic alleles decreased with increasing reproductive rate.

This might be because the number of individuals in a patch with more altruists was larger than in a patch with less altruists, so that the number of individuals in altruistic patches might fluctuate more when reproductive rates are high.

Previous theories suggest that reduced migration increases genetic variation among groups so that interdemic group selection is more likely to occur when migration rates are low. Aoki (1982) showed that the condition for group selection to prevail over counteracting individual selection is $nm < k/(2s)$, where n is the size of each deme, k is a measure of the intensity of group selection, m is the migration rate and s is the selection coefficient against the altruistic allele. Kimura (1983) also reached a similar conclusion by using a diffusion model. However, several authors (Maynard Smith, 1976; Skatkin, 1985; Harrison and Hastings, 1996) have suggested that interdemic group selection is unlikely in nature because low gene flow or migration is required for divergence among groups and high extinction rates, but this simultaneously reduces the chances of recolonization and the spread of alleles which are beneficial for groups.

The present results indicate that selective extinction is the most effective means of increasing the frequencies of altruistic alleles when there is no migration among groups. However, when there is no migration, there is no chance of recolonization and the formation of new groups. In my simulation, when $\sigma_d = 20$ and $K = 16$, there was no new group formation; only one or two groups survived until the 500th generation. If the extinction rate is not zero and no new groups form, all groups will be subject to extinction, and such organisms cannot survive. Thus, pure interdemic group selection (i.e. evolution by turnover of groups) will be difficult unless there are high extinction rates and high migration rates only after the extinctions. However, in the present simulation, when dispersal distance (σ_d) was >50, the numbers of recolonizations were nearly equal to the numbers of extinctions. Extinctions and recolonizations (i.e. interdemic group selection), together with 'effective migration', have a significant effect when dispersal distance is moderately low. Such conditions may possibly be achieved in some organisms, although more information is required about the nature of dispersal, population turnover and variation among groups.

Some authors have clearly distinguished between interdemic and intrademic group selection and have suggested that intrademic group selection is more likely to occur than interdemic group selection (Wilson, 1977, 1983; Wade, 1978). However, intrademic and interdemic group selection might not be so clearly distinguished. For instance, 'effective migration' can occur either into patches after extinctions or into surviving patches. The former constitutes recolonization, whereas the latter does not, although the effect of the migration does not differ between the two cases. In addition, consider a case where the population size in a patch decreases to two or three individuals but the population recovers by adding immigrants. This may be similar to the process in which the population becomes extinct but recovers with the help of immigrants. Thus, intrademic and interdemic group selection could be similar processes in some cases. As mentioned above, a pure interdemic selection process is difficult to achieve, but the mixing effect of inter- and intrademic selection may play a significant role in evolution.

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