

POPULATION DEMOGRAPHY AND THE EVOLUTION OF HELPING BEHAVIORS

LAURENT LEHMANN,^{1,2} NICOLAS PERRIN,^{3,4} AND FRANÇOIS ROUSSET^{5,6}

¹*Department of Genetics, University of Cambridge, Downing Street, Cambridge CB2 3EH, United Kingdom*

²*E-mail: ll316@cam.ac.uk*

³*Department of Ecology and Evolution, University of Lausanne, Le Biophore, CH-1015 Lausanne, Switzerland*

⁴*E-mail: Nicolas.Perrin@unil.ch*

⁵*Laboratoire Génétique et Environnement, Université de Montpellier II, Place Eugène Bataillon, 34095 Montpellier cedex 05, France*

⁶*E-mail: rousset@isem.univ-montp2.fr*

Abstract.—Limited dispersal may favor the evolution of helping behaviors between relatives as it increases their relatedness, and it may inhibit such evolution as it increases local competition between these relatives. Here, we explore one way out of this dilemma: if the helping behavior allows groups to expand in size, then the kin-competition pressure opposing its evolution can be greatly reduced. We explore the effects of two kinds of stochasticity allowing for such deme expansion. First, we study the evolution of helping under environmental stochasticity that may induce complete patch extinction. Helping evolves if it results in a decrease in the probability of extinction or if it enhances the rate of patch recolonization through propagules formed by fission of nonextinct groups. This mode of dispersal is indeed commonly found in social species. Second, we consider the evolution of helping in the presence of demographic stochasticity. When fecundity is below its value maximizing deme size (undersaturation), helping evolves, but under stringent conditions unless positive density dependence (Allee effect) interferes with demographic stochasticity. When fecundity is above its value maximizing deme size (oversaturation), helping may also evolve, but only if it reduces negative density-dependent competition.

Key words.—Allee effect, altruism, demographic stochasticity, environmental stochasticity, kin selection, recolonization.

Received November 28, 2005. Accepted April 1, 2006.

Behaviors by which an individual sacrifices a fraction of its resources or itself to the benefit of another individual are of central importance to the evolution of sociality. Evaluating the conditions under which such behaviors are selected for requires a careful account of how the behavioral effects translate into fitness costs and benefits. A considerable amount of theoretical work has been devoted to this issue, usually under the heading of “evolution of altruism.” Inclusive fitness theory (Hamilton 1964) emphasizes that altruism may evolve if recipient individuals tend to bear the genes underlying the behavior. Thus, genetic relatedness between actor and recipients matters for the evolution of such behaviors. However, it has been more recently emphasized that genetically related neighbors are also more strongly competing for the same local resources, which could at least partially offset the fecundity benefits to neighbors. Indeed, in a simple model where relatedness between group members is induced by population structure, the direction of selection on helping is determined solely by direct fecundity benefits, the behavior being selected for only if the actor’s fecundity, that is, the number of juveniles counted before any competition stage, is increased (Taylor 1992a). This result takes the form $B/N - C > 0$, where N is the group size, C is the fecundity cost of the act, and B is the total fecundity benefit to the group, including the actor, so that a benefit B/N is received by the actor.

Taylor’s model assumes a fixed number of adults. With this assumption, the behavior may affect the fecundity or survival of some individuals, but the demographic consequences on, for example, patch survival or growth, are ignored by construction. Thus, it might be felt that such models ignore an important component of group selection. Indeed, a helping behavior that enhances the group members’ fecun-

dity might result in an expansion of adult group size, thereby increasing group fitness so that helping is eventually selected for. Various demographic situations can accommodate the expression of such demographic sensitivity, defined as a change in group size caused by a change in behavior. If, for instance, demographic stochasticity maintains patches undersaturated, then an increase in fecundity or a decrease in mortality may translate into higher average group size, closer to the deme carrying capacity. Another example occurs under metapopulation dynamics, when helping decreases extinction rates of local patches or increases colonization rate of empty patches, thereby enhancing the equilibrium occupancy rate.

A few theoretical studies have investigated the effect of population sensitivity on the evolution of helping. The effect of environmental stochasticity was studied through simulations by Mittleldorf and Wilson (2000). In this model individuals are living on a lattice, interact locally, and environmental disturbances occur randomly through the introduction of vacant breeding sites in each generation. However, an artificial fecundity is attached to vacant sites so that they can reproduce and thus take the place of an occupied patch. Empty breeding sites can thus be seen as another species competing against the resident species in which a helping and a defector allele segregate. These peculiar assumptions make the biology of the model unclear and the results difficult to interpret and compare with Taylor’s model. By contrast, the effect of demographic stochasticity on the evolution of helping was investigated through heuristic approximations by Van Baalen and Rand (1998) and Le Galliard et al. (2003). These works use moment closure approximations under a stepping stone model. In addition, their scenario differs in many ways from Taylor’s initial model, for example assum-

ing overlapping generations, a feature known in itself to affect the $B/N - C > 0$ rule (Taylor and Irwin 2000).

While helping seems to be favored in the setting of these works, many uncertainties remain concerning the effect of population sensitivity on its evolution. The present work aims at a more direct evaluation of the effect of environmental and demographic stochasticity on the $B/N - C > 0$ rule, as our models are more directly comparable with Taylor's (1992a). We address the evolution of helping—defined here as a behavior that increases the group's fecundity and/or survival—in the presence of these two kinds of stochasticity independently. Our aim is not simply to check whether stochasticity favors helping, but to compare different modes of stochasticity, dispersal, and helping to highlight which ones are more conducive to the evolution of the behavior. We will refrain from any discussion of "altruism" until our conclusion because, according to some definitions at least, "altruism" is defined from effects on fitness that depend in a complex way on the parameters from which helping behavior is defined. Hence, we do not necessarily equate altruism and helping. We are interested in the conditions under which a behavior is favored by selection or not, independently of whether this behavior should qualify as altruistic.

First, we will consider that fecundity is large enough so that demes immediately return to a ceiling patch size after extinction and recolonization, and ask whether helping is selected for when environmental disturbances occur independently in each patch. We contrast the consequences of two modes of recolonization on the spread of helping (propagule vs. migrant pool model; Slatkin 1977). This distinction is expected to matter because the two models lead to different levels of kin competition. We then investigate the effect of the behavior on the probability of deme extinction. Our results show that these processes affect Taylor's rule in a way that increases selection on helping.

Next, we will consider the effect of demographic stochasticity on helping in the presence of two modes of density-dependent regulation. First, under ceiling regulation, demes are repeatedly driven below saturation by demographic stochasticity so that the benefits of helping allow expanding average deme size. However, the results suggest that deme size and fecundity and/or survival must be very low for the $B/N - C > 0$ rule to be notably affected, unless Allee effects are also in operation. Second, we consider that regulation acts through density-dependent survival of juveniles, which allows deme size to fluctuate around an average determined by an interaction between adult reproduction and juvenile mortality. Helping can spread by increasing fecundity only insofar that demes are undersaturated. By contrast, helping can be favored at all values of deme saturation if the behavior results in a relaxation of the intensity of competition. Our results thus suggest that Taylor's rule is substantially affected in this situation.

Finally a relatively simple modification of Taylor's result is proposed to account for the effects of demographic stochasticity. While this modified rule is not the most exact result we will obtain, it may provide a good balance between the accuracy of predictions and the amount of information required to evaluate it.

MODEL

Table 1 provides a list of symbols used in the model.

Life Cycle

We assume that evolution occurs in a haploid population where individuals are living in demes of finite size n . The life cycle is the following: (1) Independent demic extinctions result from environmental disturbances with probability $1 - s_d$. (2) Reproduction occurs in surviving demes. Individual fecundities follow independent Poisson distributions, so that the average number of offspring produced in a deme is also Poisson distributed. Adults then die. (3) Each juvenile disperses independently from each other with probability d to another random deme. Accordingly, the average number of juveniles in a deme after dispersal is also Poisson distributed, with mean denoted λ_n . (4) Each juvenile survives density-dependent regulation with a probability s_c that may depend positively (Allee effect) or negatively on local density. Thus, a deme of size n in the parental generation can reach any size n' in the descendant generation, as a result of stochastic events affecting independently the reproduction of parents and the survival of offspring. Additionally, negative density dependence may also act by culling juveniles when their number exceeds a ceiling patch size N_{\max} . When this is the case, a deme of size n in the parental generation can reach any size $n' \leq N_{\max}$ in the descendant generation. Demographic stochasticity can be prevented to occur in this case by letting the mean fecundity become infinitely large so that deme size is always equal to the ceiling size N_{\max} .

A variant of the above life cycle will be considered under environmental stochasticity, corresponding to the metapopulation models of Slatkin (1977), in which extinct demes are recolonized directly after extinction and before dispersal. This implies two rounds of dispersal: a first one for recolonization of empty demes, and a second one for migration between nonextinct demes. Recolonization occurs according to either the migrant pool model, where individuals compete against each other for access to breeding spots in extinct demes, or the propagule pool model, where extinct demes are recolonized by propagules of N_{\max} individuals formed within demes before the dispersal phase. These propagules compete against each other for access to whole demes. In other words, two types of offspring are produced: those that disperse by groups of size N_{\max} to colonize extinct demes, and those who disperse (or not) independently in nonextinct demes. In Slatkin's original formulation, the propagule size could be any value $\leq N_{\max}$ and deme size was brought back to N_{\max} by an additional round of reproduction at recolonization, but this is not assumed here. Differences between the migrant pool and propagule pool model can be described by the parameter ϕ denoting the probability that recolonizers come from the same deme. In the migrant pool model, $\phi = 0$, while in the present version of the propagule pool model, $\phi = 1$.

To determine whether helping will spread in such a population, we introduce a two-allele model. The individuals that bear one allele (denoted A) express an act that reduces their fecundity by some cost C . We assume that this act can have an effect on three different parameters of the life cycle de-

TABLE 1. List of symbols.

Symbol	Definition
n	Deme size in the parental generation
n'	Deme size in the descendant generation
N_{\max}	Ceiling deme size
N_{eq}	Average deme size at demographic equilibrium
g	Number of juveniles entering in competition in a deme
d	Dispersal rate (forward migration rate)
m	Backward migration rate (probability that an individual sampled in a deme after dispersal is an immigrant)
ϕ	Probability that two recolonizers descend from the same deme
s_d	Deme survival probability during environmental disturbances
s_c	Juvenile survival probability during competition
s_s	Juvenile survival probability during competition in the absence of any density-dependent effect
a_s	Juvenile survival parameter allowing for the expression of an Allee effect
k_s	Parameter describing the strength of negative density dependence
C	Fecundity cost of a helping act
B	Effect of a helping act on the fecundity of a deme
D	Relative effect of a helping act on deme survival
\bar{D}	Relative effect of a helping act on the parameter k_s
p	Frequency of the mutant allele in the population
$w(n', n)$	Fitness function defined as the expected number of adult offspring (in a deme of size n') descending from a focal individual breeding in a deme of size n
$f(n', n)$	Frequency function ($f[n', n] \equiv w[n', n]n/n'$)
z_{\bullet}	Phenotype of a focal individual
z_0^R	Average phenotype of individuals from the focal deme
z_1	Average phenotype of individuals from different demes
b	Baseline fecundity
b_{\bullet}	Fecundity of the focal individual
b_0	Average fecundity in the focal deme
b_1	Average fecundity in different demes
Q_0^R	Relatedness between a focal individual and a randomly sampled individual (including the focal) from its group
$Q_0^D \equiv F_{\text{ST}}$	Relatedness between a focal individual and another individual from its group
S	Inclusive fitness effect
S_f	Weighted effect of actors on the expected number of adult offspring of focal individuals
S_{Pr}	Weighted effect of actors, through changes in the demographic states of the population, on the reproductive value of offspring of focal individuals
dN_{eq}/dz	Population sensitivity defined as a change in group size caused by a change in behavior
$v(n)$	Relative reproductive value of a deme of size n
\mathbf{P}	Transition matrix of the Markov chain describing deme demography
\mathbf{p}	Stationary distribution of the Markov chain
\mathbf{Z}	Fundamental matrix of the Markov chain

scribed above. First, the act can increase the survival probability (s_d) of the deme during environmental disturbances by an effect D/n , where n is the number of individuals in the deme. Second, The act may increase the survival probability (s_c) of competing juveniles in the deme after dispersal. The density-dependent survival probability of such a juvenile is assumed to be

$$s_c(g) = s_s g^{a_s} e^{-k_s(g-1)}, \quad (1)$$

where g is the total number (random) of juveniles coming in competition. The values of the parameters s_s , a_s , and k_s fine-tune the shape of the survival probability function (see Fig. 1). The parameter s_s can be interpreted as the survival probability of a juvenile in the absence of any density dependence. An Allee effect may occur if $a_s > 0$ and k_s describes the strength of negative density dependence. We assume that the helping act reduces k_s by a relative effect $[\bar{D}]/n$. Consequently the survival of all juveniles, whether philopatric or immigrant, is increased similarly by the level of helping in the group. This effect of helping can be thought of as an effect on deme carrying capacity, which is defined here as the average deme size at demographic equilibrium.

Finally, the act may also increase the overall fecundity of the group by B , and we will consider two different situations of how this benefit is distributed among the members of the group. First, the act may increase the fecundity of each individual in the group, including the actor, by B/N as in Taylor's original model. Second, the act may increase the fecundity of each individual, but excluding the actor, by $B/(N - 1)$. In this latter case, Taylor's result takes the form $-C > 0$ because the actor receives no share of the benefits generated by its act. When n fluctuates, the total effect on the focal individual's fecundity varies with deme size in the first case, whereas it is a constant in the second case.

Measuring Selection on Helping

Because we consider an infinite island model of dispersal, the change in allele frequency (p) for a mutant with phenotypic effect δ over one generation can be written $\Delta p = \delta S / p(1 - p) + O(\delta^2)$, where $O(\delta^2)$ is a residue of order δ^2 (Rousset 2004, pp. 206–207). Accordingly, there is a measure S determining the direction of selection at any allele frequency under weak selection. The expression $\Delta p = \delta S p(1 - p) +$

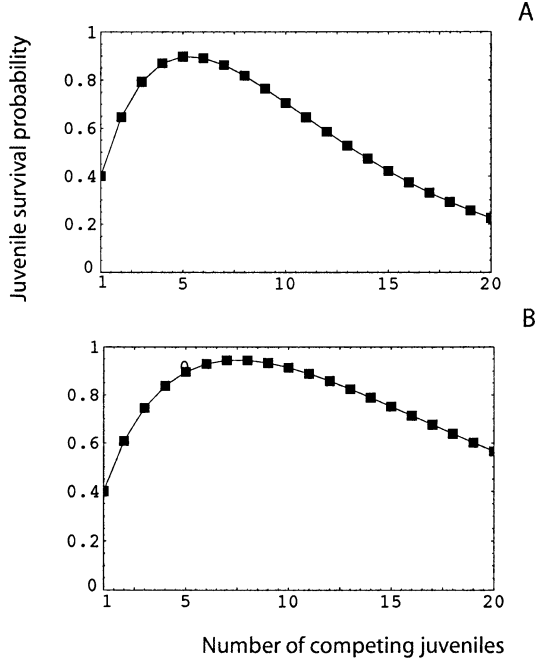


FIG. 1. Probability of juvenile survival $s_c(g) = s_s g^{a_s} e^{-k_s(g-1)}$ graphed as a function of the number g of juveniles coming in competition in a deme after dispersal. k_s describes the strength of negative density dependence. (A) Parameter values are $s_s = 0.4$, $a_s = 0.95$, and $k_s = 0.18$. (B) Parameter values are $s_s = 0.4$, $a_s = 0.75$, and $k_s = 0.1$. In both cases there is an Allee effect.

$O(\delta^2)$ implies that S fits within Hamilton's definition of the inclusive fitness effect, which is a weighted sum of the expected effects of all individuals in the population on the fitness of individuals bearing the mutant allele. In Taylor's (1992a) model, $S = (B/N - C)(1 - F_{ST})$, where F_{ST} is Wright's measure of population structure (Rousset, pp. 114, 150). This is consistent with Taylor's result that the behavior is selected for if $B/N - C > 0$. The inclusive fitness effect S can be computed by the direct fitness method (Taylor and Frank 1996; Rousset and Billiard 2000), as

$$S \equiv \frac{\partial w}{\partial z_\bullet} + \frac{\partial w}{\partial z_0^R} Q_0^R, \quad (2)$$

where $w \equiv w(z_\bullet, z_0^R)$ is a fitness function giving the expected number of adult offspring of a focal individual, and Q_0^R is the relatedness between the focal individual and a randomly sampled individual (including itself) from the focal patch. The derivatives of w are the effects of actors on the fitness of a focal individual, the actors being the focal individual itself with phenotype denoted z_\bullet , and individuals from the focal deme with average phenotype denoted z_0^R .

In a metapopulation following the island model of dispersal, generalized expressions of the measure S have to be considered because different demographic states have different probabilities of occurrence and might result in individuals having different expected contributions to the ancestry of the population. Hence, the fitness measure S also depends on the probabilities of transition in deme size and on the reproductive value of demes (see Appendix 2). The expressions for S used here are based on an exact description

of the first-order effects of selection on allele frequency change, and therefore all components of selection on mutants with small effect are taken into account, whether these are described as individual, kin, or group selection. The reproductive value weights measure the differences in expected future contribution of offspring according to the different types of demes they settle in. They are obtained as the weights that ensure that a neutral mutant (without phenotypic effect) does not change in weighted frequency over one generation, regardless of its frequency among the different types of demes in the previous generation. We refer the readers to Rousset and Ronce (2004) for proofs and independent simulation tests. With environmental stochasticity, the first fitness expressions comparable to those of Rousset and Ronce (2004) are those of Comins et al. (1980), whose results are also consistent with the present ones. While Comins et al. assumed that each deme is either empty or full, this is relaxed in Rousset and Ronce (2004). Although Taylor (1992b, eq. 4) wrote some fitness expression for what he called an "elastic" environment, it is unclear how these expressions relate to allele frequency change. For example, difference in expected future contribution (reproductive value) of offspring in demes of different size are not taken into account.

The fitness measure can generally be decomposed into two terms:

$$S = S_f + S_{Pr}. \quad (3)$$

S_f is the weighted effect of actors on the expected number of adult offspring of focal individuals. In a population of constant size, this is the term that yields Taylor's result. S_{Pr} is the average effect of actors, through changes in the demographic states of the population, on the reproductive value of these offspring. In the present context, the reproductive value of offspring depends on the size of the deme they settle in, and S_{Pr} takes into account the variation in offspring reproductive value through the effect of actors on deme size in the next generation.

Fitness Function and Deme Transition Probabilities

We describe here the fitness functions, necessary to evaluate S , in the case of environmental stochasticity only. The more complex expressions for demographic stochasticity are detailed in Appendix 2.

In the presence of environmental disturbances, we allow the extinction probability to depend on the behaviour of deme members, such that the probability that a focal deme does not go extinct is $s_d(1 + Dz_0^R)$. Then, a focal individual produces $(1 + Bz_0^R - Cz_\bullet)b$ offspring, where b is the baseline fecundity. Both deme survival and individual fecundity may be functions of the average phenotype z_0^R in the focal deme. The superscript emphasizes that the phenotype of the focal individual z_\bullet is included in the average. A fraction $1 - d$ of the offspring of the focal individual remain philopatric. These offspring compete with $(1 - d)[1 + (B - C)z_0^R]b$ juveniles produced in the focal deme and $s_d(1 + Dz_1)[1 + (B - C)z_1]db$ immigrant juveniles; z_1 is the average phenotype in different demes. A complementary fraction d of the offspring of the focal individual disperse. With probability $(1 + Dz_1)s_d$ the dispersing progenies compete in nonextinct demes with res-

ident and immigrant juveniles. With complementary probability, the dispersing progenies compete in extinct demes with other immigrant juveniles. Collecting all the above terms gives the fitness function

$$w = \sigma(z_0^R) \left\{ \frac{(1 - m)b_\bullet}{(1 - m)b_R + mb_d} + \frac{[1 - \sigma(z_1)]b_\bullet}{\sigma(z_1)b_d} + \frac{mb_\bullet}{b_d} \right\}, \quad (4)$$

where $\sigma(x) \equiv s_d(1 + Dx)$, so that $\sigma(z_0^R)$ denotes the probability of survival of the focal deme and $\sigma(z_1)$ that of a different deme; $b_\bullet \equiv (1 + Bz_0^R - Cz_\bullet)b$ is the focal individual's fecundity; $b_R \equiv [1 + (B - C)z_0^R]b$ is the average fecundity in the focal deme; $b_d \equiv [1 + (B - C)z_1]b$ is the average fecundity in different demes; and $m \equiv d\sigma(z_1)/[(1 - d) + d\sigma(z_1)]$ is the backward migration rate (i.e., probability that an individual sampled after dispersal in a deme is an immigrant). When the fecundities of all classes of individuals is set to b , equation (4) reduces to equation (B.4) in Gandon and Michalakis (1999) under the assumption that the population is monomorphic for dispersal and that individuals disperse randomly to other demes (island model).

As described in the Life Cycle section, in the propagule pool model, there are two types of offspring produced: those who disperse by groups of N_{max} to colonize extinct demes, and those who disperse independently in nonextinct demes (or do not disperse). We assume that both types of juveniles are produced in proportion to the fecundity of individuals as it is affected by all actors' behavior. Thus, the number of propagules produced by a deme is proportional to the average fecundity in the deme, and the individual contribution to the propagule is proportional to the individual fecundity relative to the deme fecundity. Under these assumptions, the fitness function of a focal individual is also given by equation (4).

RESULTS

Environmental Stochasticity

In this section we investigate the effect of environmental stochasticity ($s_d < 1$) alone on the evolution of the helping behavior. Accordingly, demographic stochasticity is prevented by assuming a very large fecundity ($b \rightarrow \infty$). Under this assumption, the inclusive fitness effect S takes the form

$$S = \underbrace{-C + BQ_0^R - (B - C)(1 - m)^2 s_d Q_0^R}_{S_f} + \underbrace{Ds_d Q_0^R}_{S_{Pr}}, \quad (5)$$

(eq. A1 in the Appendix). S_f may be understood as the effect of the behavior on the expected number of adult offspring of the focal individual in demes of given total size N_{max} . This effect depends on the direct cost of helping, the benefits from individuals expressing helping in the focal deme (including the focal individual itself), and the increase in competition in the focal deme resulting from such helping. S_{Pr} measures the effect of the behavior on the probability of survival of the focal deme and is a net benefit. We now discuss the different variants of our life cycle in the light of equation (5).

The mutant allele affects deme fecundity

In the absence of any effect of the behavior on the probability of deme survival ($D = 0$), we can substitute the ex-

pression for Q_0^R (eq. A4) into the expression for S (eq. 5) to obtain the condition for the spread of helping, $S > 0$, in the form

$$B \left\{ \frac{1}{N_{max}} + \left(\frac{N_{max} - 1}{N_{max}} \right) \times \frac{\phi(1 - s_d)}{[1 - (1 - m)^2 s_d] N_{max} - \phi(1 - s_d)(N_{max} - 1)} \right\} - C > 0. \quad (6)$$

The fitness benefit varies directly with the probability of common origin and the extinction rate and inversely with the migration rate and group size.

Under the migrant pool mode of recolonization, individuals recolonize extinct patches at random. In our infinite island model of dispersal this implies that the probability of common origin ϕ of two individuals is set to zero. Then, the inclusive fitness effect given by equation (6) reduces to $S = (B/N_{max} - C)(1 - Q_0^R)$ where $Q_0^R \equiv F_{ST}$ is the relatedness between the focal actor and another individual from its group. Thus, we recover Taylor's result, which holds when the fecundity of each individual in the group (including the actor) is increased by B/N_{max} .

Under the propagule pool mode of recolonization, individuals recolonizing extinct patches all originate from the same deme. In our infinite island model of dispersal this implies that the probability of common origin ϕ of two individuals is set to one. The condition for the spread of helping given by equation (6) then takes the form

$$B \left\{ \frac{1}{N_{max}} + \left(\frac{N_{max} - 1}{N_{max}} \right) \frac{1 - s_d}{1 - s_d[1 - m(2 - m)N_{max}]} \right\} - C > 0. \quad (7)$$

We can see from this inequality that in the propagule mode of recolonization, Taylor's result is notably affected, so that the spread of helping is facilitated. This is a consequence of the assumptions that propagules recolonize randomly extinct demes and that kin competition is absent during recolonization. Therefore, when a deme produces more propagules as a result of the helping behavior, it is also more likely to recolonize extinct demes. The helping trait can then be successfully exported from one deme to the next. In the absence of environmental disturbances ($s_d = 1$), we recover Taylor's result because dispersal between nonextinct demes follows the migrant pool mode.

We will also consider the situation where the actor increases the fecundity of its $N_{max} - 1$ neighbors by an amount B . The selective pressure on helping in this situation can be obtained by replacing Q_0^R by Q_0^B in the second term of S_f in equation (5), which represents the benefits from helping in the focal deme. Then, the condition for the spread of the behavior in the propagule pool model ($\phi = 1$) is:

$$B \frac{1 - s_d}{1 - [1 - m(2 - m)N_{max}]s_d} - C > 0. \quad (8)$$

When $m \rightarrow 0$, dispersal in the metapopulation occurs only through recolonization of extinct patches by propagules and the condition for the evolution of helping further reduces to

$B - C > 0$. Under this assumption of no genetic exchange between demes all individuals within demes will ultimately become identical. Then, demes can be interpreted as functioning as a reproducing unit, individuals as cells, propagules as gametes, and $B - C$ as the selective advantage of an allele as considered in standard population genetic theory.

The critical assumption that leads to the evolution of helping in the propagule pool model of recolonization is that competition occurs between propagules for access to whole demes, and in particular not between individuals within each propagule. Alternatively, individuals might compete for access to breeding spots. In this case, the direction of selection on helping is given by Taylor's rule because kin competition occurs also in patches that are recolonized (eq. A6). Indeed, the accrued fecundity benefits of helping resulting from the increased relatedness obtained through propagule recolonization also boost kin competition among immigrants. Both effects cancel each other, so that Taylor's result holds independently of the extinction probability of demes and the probability of common origin of individuals recolonizing extinct demes.

The mutant allele affects deme survival

In the previous section we assumed that the environmental extinction rate of demes was independent of the helping trait. We now let deme survival s_d be a function of the behavior under selection, that is, $D > 0$. The condition for the spread of helping is also obtained by plugging the expression for Q_0^R (eq. A4) into the one for S (eq. 5). For the migrant pool mode of recolonization ($\phi = 0$), the trait is selected for when

$$D/N_{\max} + (B/N_{\max} - C)[1 - (1 - m)^2 s_d] > 0 \quad (9)$$

is satisfied. A helping behavior reducing deme extinction can be selected for even in the absence of fecundity benefits, that is when $B = 0$. In this situation, the condition under which the behavior spreads is:

$$\frac{D}{[1 - (1 - m)^2 s_d] N_{\max}} - C > 0. \quad (10)$$

The benefit of reducing deme extinction varies directly with the deme survival rate and varies inversely with the migration rate. Under complete dispersal ($m \rightarrow 1$), the inequality reduces to $D/N_{\max} - C > 0$. Whether helping will be selected for then depends only on the effect of the focal individual on its fitness. As usual, when dispersal decreases, genetic identity increases between individuals, thus promoting kin selection. Here kin interactions have positive effects on the fitness of the focal individual, which facilitate the evolution of helping.

Demographic Stochasticity

To evaluate the effect of demographic stochasticity on the evolution of helping, we assume that migration is random ($\phi = 0$) and that the behavior has no influence on the patch disturbance probability ($D = 0$). Then, the inclusive fitness effect on helping when the act increases the fecundity of each member of the group is

$$S = \underbrace{\sum_n (B/N - C)[1 - Q_0^D(n)]\alpha(n)}_{S_f} + S_{Pr}, \quad (11)$$

which is obtained by substituting equation (A18) into equation (3). Here S_f is a weighted average of terms $B/n - C$, each analogous to the result in Taylor's model ($S = B/N - C$). The weights are function of the relatedness $Q_0^D(n)$ between different individuals within demes of size n , and of the reproductive value $\alpha(n)$ of all demes of size n . Thus, S_f may be maximized for some distribution of deme size that depends on a trade-off between the benefits of helping ($B/n - C$, higher in small demes) and the relatively low reproductive value of small demes.

S_{Pr} measures the effect of the behavior on the reproductive value of philopatric offspring, through changes in the demography of the focal deme. As S_f does, it depends on the reproductive value of offspring in the focal deme and on probabilities of genetic identity. In addition, S_{Pr} depends on the effects of helping by the different actors on the probabilities of occurrence of any focal deme size in the offspring generation given focal deme size in the parental generation. In contrast to S_f , no simplified expression was found for S_{Pr} relative to its general form. Nevertheless, we show in the Appendix 2 that the sign of S_{Pr} involves the covariance between the reproductive value of the whole set of juveniles in the focal deme and the size of that deme in the descendant generation. When the reproductive value of a deme increases with its size, which seems to be generally the case under ceiling regulation, the demographic effects of the behavior have a positive feedback on its evolution ($S_{Pr} > 0$). In this situation, helping will simply enhance the degree of saturation of the patch, eventually reaching the point where the fecundity is large enough so that it cancels demographic stochasticity because all individual breeding spots will be occupied. More generally, the effect of the behavior on S_{Pr} will depend on the particular mode of density-dependent competition between juveniles (eq. 1 and Fig. 1). Situations might then arise where the deme reproductive value (i.e., the reproductive value of all deme members) decreases when fecundity exceeds a saturation threshold. If, for instance, juvenile survival drops sharply at high density owing to food shortage, an increase in fecundity might actually boost patch extinction. Patch reproductive value will then covary negatively with offspring number. A helping behavior favoring a too large fecundity will then be selected against through its negative effect on the demography of the group ($S_{Pr} < 0$).

Numerical analysis shows that the sign of the selective pressure S_{Pr} is well predicted by the sign of the sensitivity of population size to the behavior (Fig. 2). Population sensitivity indicates whether average patch size will grow or shrink as a result of helping getting fixed in the population (see Appendix 3). When helping results in group expansion ($dN_{eq}/dz > 0$), it is selected for through its effect on the demography of the patch ($S_{Pr} > 0$); conversely, helping will be selected against if the resulting additional fecundity reduces adult deme size. A positive selective pressure on the trait resulting from its effect on deme demography ($S_{Pr} > 0$) thus tends to favor larger deme size, but selection on helping

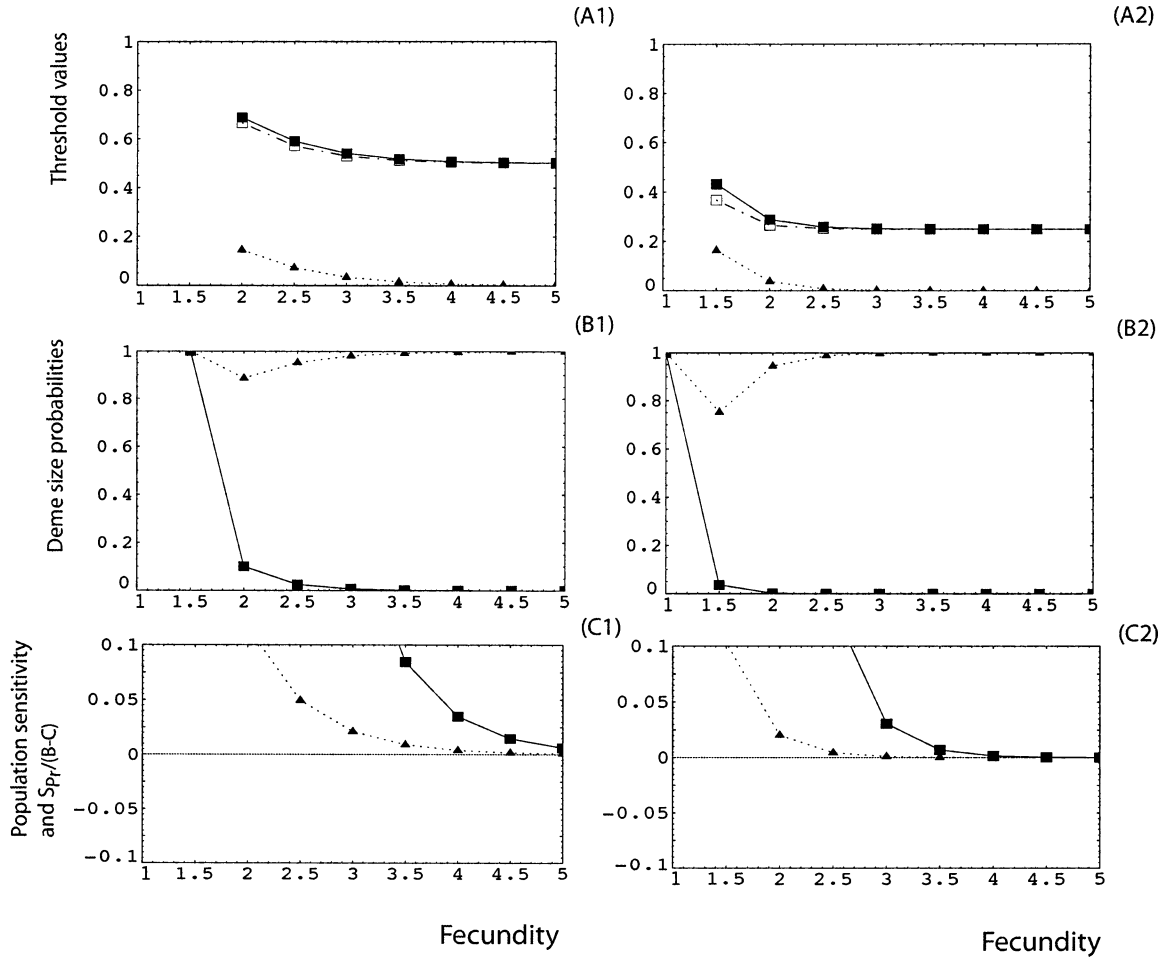


FIG. 2. Selective pressure on helping and patch demography as a function of fecundity under ceiling regulation. (A) Threshold values κ so that selection favors helping when $C/B < \kappa$. Triangles stand for κ when helping increases the fecundity of all individuals in the deme but excluding the actor and black squares stand for the case where the fecundity of each individual including the actor is increased. Open squares (matching black squares) stands for the approximation of κ in the latter situation (eq. 12). (B) Black squares stand for the probability that a focal deme is extinct, and triangles stand for the probability that it is either extinct or at the ceiling patch size (N_{\max}). (C) Black squares stand for the standardized population sensitivity, $(dN_{\text{eq}}/dz)/(B - C)$ and triangles stand for the standardized effect of helping on patch demography, $S_{Pr}/(B - C)$. Parameters values are $N_{\max} = 2$ for panels A1, B1, and C1 and $N_{\max} = 4$ for panels A2, B2, and C2, and the dispersal probability is $d = 0.1$ for all figures.

will generally not drive population size to a maximum, as it depends on the total inclusive fitness effect ($S_f + S_{Pr}$).

The mutant allele affects deme fecundity

To evaluate the sign of the measure of selection S for a given fecundity cost-to-benefit ratio as a function of the remaining parameters of our model, we seek numerically the threshold value κ of the ratio C/B such that $S = 0$. Selection then favors the trait when $C/B < \kappa$; this threshold can be calculated analytically for all models presented in the section Environmental Stochasticity. We will compare the threshold κ values under the two different modes of distribution of B among the members of the group. First, we consider the case where the benefit is shared by all individuals in the patch but excluding the focal actor (in this case κ is undefined for demes of constant size N , because $S \propto -C$). Second, we assume that the benefit B is shared equally by all individuals in the group, including the focal actor (in this case $\kappa = 1/N$ for demes of

constant size N , because $S \propto B/N - C$). In this latter situation, the threshold value is well approximated by the weighted harmonic average

$$\kappa \approx \frac{\sum_{n>0} \{[1 - Q_0^P(n)]\text{Pr}(n)/n\}}{\sum_{n>0} [1 - Q_0^P(n)]\text{Pr}(n)}. \tag{12}$$

In this approximation the variation in reproductive values between nonempty demes is ignored. Relatedness is still considered, as ignoring it yielded poor results. Because relatedness is easy to evaluate by routine assessment of genetic structure, while reproductive value would be harder to evaluate, equation (12) also points to ways to evaluate cost-benefit thresholds in natural populations.

In Figure 2 we compare the different threshold values and show the distribution probabilities of deme sizes under ceiling regulation. All threshold values decrease with an increase

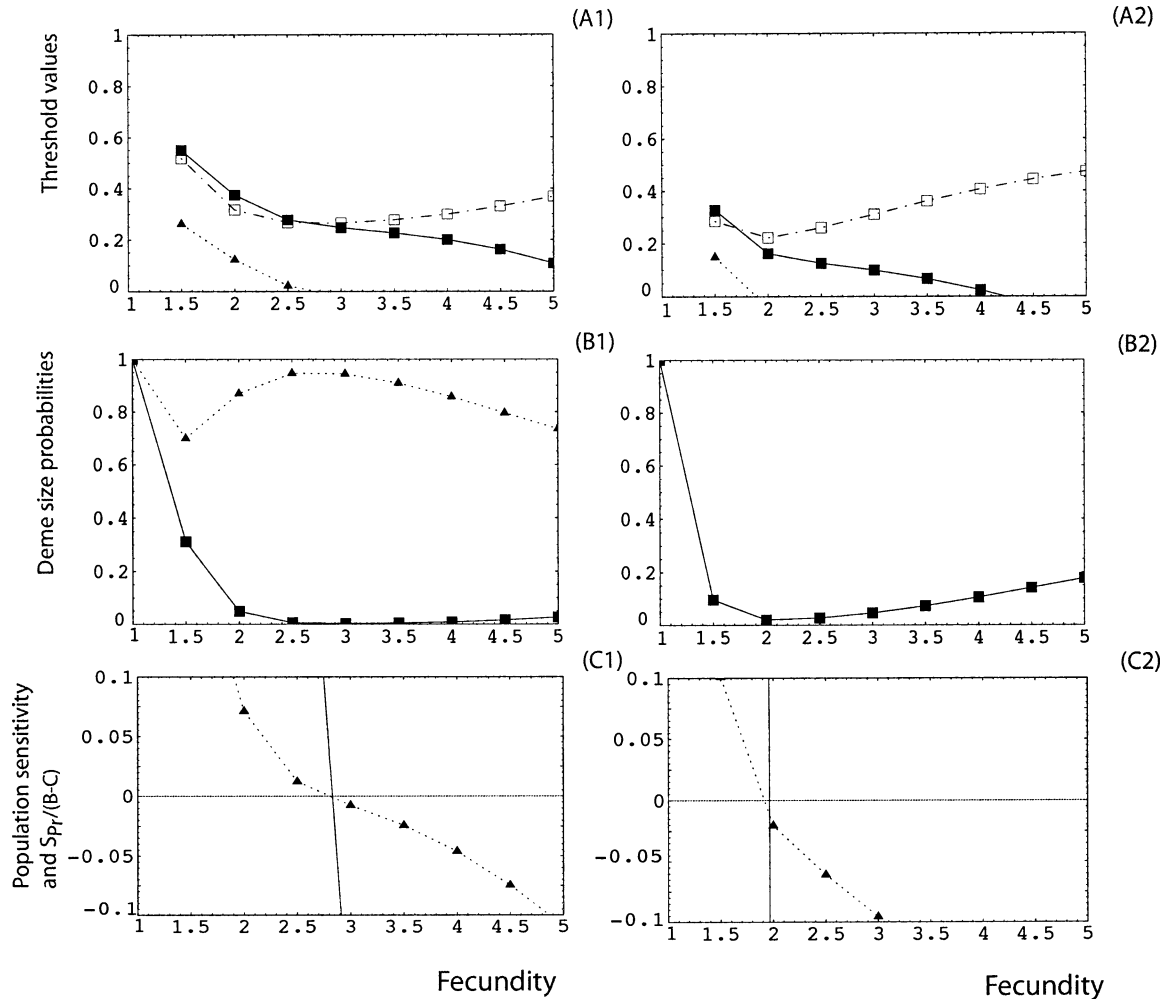


FIG. 3. Selective pressure on helping and patch demography (as in Fig. 2) under regulation through density-dependent survival of juveniles. The shape of the survival probability function of juveniles (s_c), which includes an Allee effect and negative density dependence, is given in Figure 1A and the dispersal probability is $d = 0.1$. Panels A1, B1, and C1: with ceiling patch size $N_{max} = 4$. Panels A2, B2, and C2: without ceiling patch size. In this situation, a deme can potentially take any size and will fluctuate around an average (given in Fig. 4B), which is determined entirely by the density-dependent survival probability of juveniles. In the absence of ceiling regulation, demographic stochasticity is reduced for low values of fecundity (B1 vs. B2) because average deme size is not prevented to exceed the ceiling size and is thus generally larger for the same fecundity values.

in fecundity (Fig. 2, panels A1, A2), which under the present mode of regulation dampens fluctuations in deme size (Fig. 2, panels B1, B2). Thus, as long as demographic stochasticity allows for patch expansion, helping is selected for through its positive effect on patch growth, because a larger size reduces the probability of extinction. When fecundity becomes large enough so that demographic stochasticity vanishes, the average deme size converges to the ceiling patch size ($N_{eq} \rightarrow N_{max}$). Then, the cost-to-benefit ratio that allows for the evolution of helping cannot exceed the inverse of ceiling patch size ($\kappa \rightarrow 1/N_{max}$) so that we recover Taylor's result. When the focal actor gets no share of the benefits, the threshold ratio is undefined because the selective pressure on helping becomes negative as fecundity increases ($S \propto -C$), helping is no longer selected for. Increasing migration mainly results in a decrease of relatedness between patch members, which weakens the selective pressure on helping. By contrast, allowing for environmental disturbances ($s_d > 0$) broadens

the range of parameter values where helping is selected by enhancing the expression of demographic stochasticity.

In Figure 3 we compare the threshold values and the probabilities of the demographic states of the focal deme when regulation occurs through positive and negative density dependence of juvenile survival (eq. A12; Fig. 1A). At low fecundity values, the reduction in juvenile survival (as necessarily occurs under the Allee effect model for juvenile survival) enhances demographic stochasticity and thereby increases the selective pressure on helping, whether or not the focal individual gets fecundity benefits from its own act (Fig. 2, panel B2 vs. Fig. 3, panel B1). At high fecundity values, by contrast, the negative density-dependence effects ($k_s > 0$) decrease the selective pressure for helping, because any additional fecundity would oversaturate the patch and decrease the resulting number of adults (Fig. 3, panels A1, A2). Negative density dependence thus has the potential to induce a monotonic increase in the threshold cost-to-benefit ratio that

must be satisfied for selection to favor helping. For given fecundity values, a point is eventually reached (Fig. 3, panels C1, C2) where helping is selected against through its negative effects on offspring adult reproductive value through effects on deme size ($S_{Pr} < 0$) while still selected for through increased focal individual's share of offspring given offspring deme size ($S_f > 0$). Selection might then favor helping ($S > 0$) while driving a reduction of average deme size ($dN_{eq}/dz < 0$).

Allowing for environmental disturbances ($s_d > 0$) broadens the range of parameter values where helping is selected for. However, while the fecundity switching point where S_{Pr} becomes negative matches very well the point where dN_{eq}/dz becomes negative in the absence of environmental disturbances (Fig. 3), we noted in additional numerical simulation (not shown) that S_{Pr} becomes negative before dN_{eq}/dz in the presence of such disturbances. Further analytical work remains to be done to clarify this point.

The approximation of κ given by eq. 12 breaks down when the fecundity increases above its threshold value maximizing average patch size. However, mutants that increase fecundity ($-C > 0$) without any effect on neighbors ($B = 0$) are selected against whenever the threshold cost-to-benefit ratio is negative (Fig. 3, panel A1), owing to too large negative S_{Pr} . Hence, the breakdown of the approximation may occur only at fecundity levels that are not expected to evolve in the first place.

The mutant allele affects deme carrying capacity

Here we evaluate the direction of selection on helping when it exerts an effect on the survival probability of competing juveniles (s_c). We consider that the helping act has no effect on the fecundity of neighbors ($B = 0$ in eq. 11) but reduces the parameter k_s , describing the strength of negative density dependence by a relative effect of magnitude \tilde{D} (eq. A12). We seek numerically the threshold value κ of the ratio C/\tilde{D} such that $S = 0$. Selection then favors the trait when $C/\tilde{D} < \kappa$.

Figure 4 presents the threshold C/\tilde{D} value below which helping is favored. Here again, helping can be favored only if it increases average deme size (N_{eq}). The selective pressure can be positive whether the deme is undersaturated (values of fecundity below the value maximizing N_{eq}) or oversaturated (values of fecundity above the value maximizing N_{eq}) because in either case helping results in more juveniles reaching adulthood. In contrast to previous cases, a positive effect on deme size can occur for any level of saturation of the focal deme and therefore for much higher fecundities than before (Fig. 4). Helping is actually all the more favored as fecundity is oversaturating, resulting in a drastic juvenile mortality.

DISCUSSION

Though helping may increase the fecundity or survival of relatives, it also increases kin competition. When the two effects counterbalance each other as in Taylor's (1992a) model, helping is selected against as soon as a fecundity cost applies to the focal actor. Overlapping generations and kin recognition offer two ways to tip the balance in favor of helping (Taylor and Irwin 2000; Perrin and Lehmann 2001).

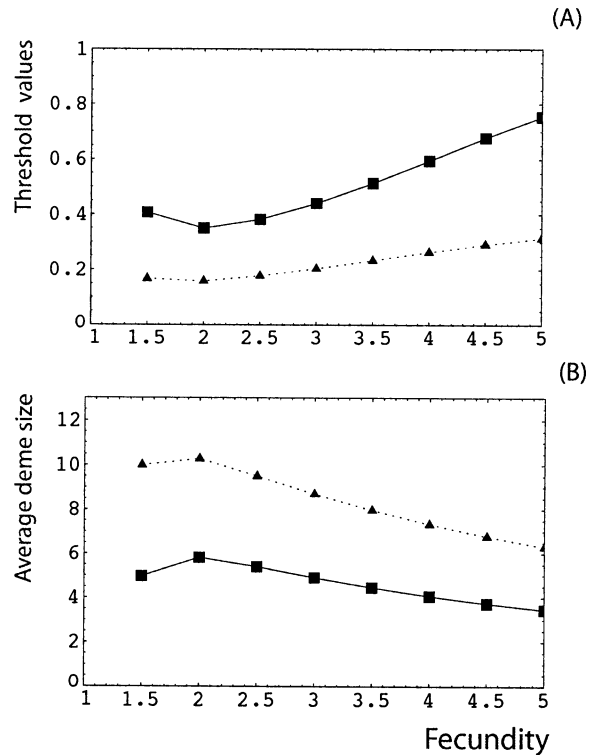


FIG. 4. (A) Threshold value κ so that selection favors helping when $C/\tilde{D} < \kappa$ in the case where helping reduces the intensity of negative density dependence affecting the survival probability of juveniles. The shape of the survival probability function for the resident trait value ($z = 0$) is given in Figure 1A for the curve with black squares and in Figure 1B for the curve with triangles. The dispersal probability is $d = 0.1$. (B) Average deme size for each case graphed in (A). The selective pressure on helping is positive but takes its lowest value for the value of fecundity that maximizes average patch size. It increases when demes are undersaturated (values of fecundity on the left of the maximum average deme size) and when demes are oversaturated (values of fecundity on the right of the maximum average deme size).

Here we have explored another way, linked to demographic sensitivity: if the behavior allows group expansion, then the kin competition pressure opposing its evolution can be greatly reduced. Both demographic and environmental stochasticity allow helping behaviors to be selected for, though with variable efficacy and under different conditions. We have found that helping is most favored when it relaxes density-dependent juvenile mortality, when it increases deme survival in the face of environmental disturbance, or when recolonization of empty patches occurs through propagules of related individuals.

Environmental Stochasticity and Modes of Deme Recolonization

Under environmental stochasticity, the benefits of helping can be directed into a higher ability of resisting patch extinction or to colonize empty patches. However, our analysis shows that Taylor's result also applies when competition occurs between individual emigrants, so that helping is favored only if recolonization follows the propagule mode. This holds because in the latter case, all related members of a propagule

settle, hence kin competition does not occur during recolonization of extinct demes. Simultaneously, relatedness is increased by the same process of recolonization by related individuals.

It is relevant in this context that the propagule pool mode of colonization is quite common among social mammals, since new groups are often produced through the fission of large ones (e.g., Gomper et al. 1998; Kays and Gittleman 2001; Waterman 2002). This pattern is particularly common in primates (e.g., Fix 1979; Scheffrahn et al. 1993; Okamoto and Matsumura 2001), where fission often occurs among lines of maternal relatedness (Lefebvre et al. 2003), which further boosts within-group relatedness. The propagule pool also represents a major mode of colonization in insect societies, whether it appears through fission, budding, or swarming (e.g., Seppa and Pamilo 1995; Chapuisat et al. 1997; Giraud et al. 2000; Fernandez-Escudero et al. 2001; Fournier et al. 2002). Fission is actually obligate in some polygynous ant species producing wingless queens (Peeters and Ito 2001).

Our analysis also shows that helping will be selected for under less stringent conditions when it increases deme survival in the face of environmental disturbances. Higher deme survival increases the competitive ability of the focal deme relative to other demes (because all individuals are more likely to reproduce) without inflating kin competition within demes. Relevant environmental disturbances may stem from either biotic or abiotic factors. The nests or burrows of social species play an important homeostatic role, buffering societies against environmental perturbations such as temperature changes (e.g., Engels et al. 1995; Starks and Gilley 1999; Starks et al. 2005). Food stores in ant or bee colonies also reduce the rise of extinction due to starvation.

Biotic sources of disturbances may stem, for example, from the attack of predators, the spread of parasites, or the aggression of individuals from other colonies. Such assaults can be better put under check with the help of altruistic or cooperative behavior (e.g., Stanford 1995; Tello et al. 2002), leading to the evolution of soldier casts in a range of eusocial species (e.g., Cooney 2002; Duffy et al. 2002; Breed et al. 2004; Kutsukake et al. 2004). It is useful to distinguish formally interspecific from intraspecific threats. While the former might be directly included into the environmental disturbance rate s_d as modeled here, the latter should be incorporated into the life cycle and should account for both the rate of aggression and the probability of resisting it, because the benefits of helping might be expressed in both of these activities. In that sense, our present model provides only a approximation of the process of warfare between groups. This process deserves a better formalization, since warfare is not uncommon among social insects or mammals, including chimpanzees and humans (e.g., Mabelis 1979; Adams 1990; Wrangham 1999; Wilson et al. 2002).

Demographic Stochasticity and Modes of Density-dependent Competition

While the effect of demographic stochasticity on the evolution on helping has been poorly investigated, existing work emphasizes its importance as an agent favoring altruism (Le Galliard et al. 2003). Our analysis confirms that demographic

stochasticity can favor the evolution of helping, but the selective pressure on the trait depends critically on its mode of action. This has been made apparent by contrasting the case where helping increases fecundity to the case where it reduces density-dependent mortality. In the latter case, the whole deme size distribution is shifted toward increased values, whatever the level of deme saturation determined by the resident allele (Fig. 4). Not only does this favor the evolution of helping, but the benefits are in fact strongest when demes are oversaturated.

Under ceiling regulation, helping is favored only to the extent that demes incur a risk of extinction as a result of low basal fecundity (Fig. 2). Thus, helping rescues the deme from extinction. Furthermore, low fecundity allows for the expression of demographic sensitivity only in small populations. Indeed, as the ceiling patch size (N_{\max}) increases, fluctuations in deme size become negligible for most of the range of fecundity values (Fig. 2). We conclude that demographic stochasticity is unlikely to select for helping in large groups under these assumptions. However, reduced juvenile survival, which necessarily occurs under our Allee effect model for juvenile survival, increases demographic stochasticity for given fecundity values (Fig. 2, panel B2 vs. Fig. 3, panel B1). Hence, the set of combinations of patch size and fecundity values for which demes incur significant extinction risks is increased. This obviously broadens the scope for the evolution of helping, to an extent that depends on the survival probability of juveniles, which is determined by an interaction between Allee effects and the mode of negative density dependence (Fig. 3, panel B1 vs. panel B2). The example of meerkats emphasize the importance of Allee effects in promoting social behavior (Clutton-Brock 2002). Adding environmental disturbances further boosts the scope for such helping to be selected for.

When helping reduces the intensity of competition for resources, the scope for its evolution is broadened. We investigated the influence of helping on this ecological constraint by letting the behavior affect the density-dependent survival probability of competing juveniles. Under this mode of regulation deme size fluctuates around an average determined by an interaction between adult reproduction and juvenile mortality, so any increase in juvenile survival through helping will shift the whole distribution toward increasing deme size. A mutant allele may then exploit this property at all levels of saturation to outpropagate its alternative (Fig. 4). This effect of helping on demography, which can be interpreted as an effect on deme carrying capacity, may be achieved through habitat and/or resource engineering.

Relevant Forms of Demographic Sensitivity

Sensitivity was defined here as any change in population size resulting from a change in the behavior of interest. Demographic sensitivity and population expansion may result from a variety of causes, of which two were investigated here (demographic and environmental stochasticity).

How the sensitivity resulting from access to new resources (niche expansion) or to new territories (range expansion) fits into our formalization deserves comment. Niche expansion will result as soon as the helping behavior allows groups to

better exploit existing resources or to obtain access to new resources. According to our results, the ensuing increase in average patch size (N_{eq}) will prevent the benefits of helping to vanish as a consequence of increased kin competition. Examples include cooperative hunting in predators (wolves, lycaons, lions, spiders; e.g., Stander 1992; Creel and Creel 1995; Boesch 2002) and more generally cooperative strategies of group foraging. The spatial distribution of some resources might prevent their exploitation by isolated individuals. Mole rats, for instance, feed on scarce underground tubercles that would be inaccessible without the digging effort of the whole colony. Our model does not specifically address these situations because the simplification we obtained for S_f (eq. 11) is based on the assumption that the average fecundity in a deme (λ_n) is density independent. However, our results suggest that selection on helping is increased as soon as it affects positively deme demography ($S_{Pr} > 0$), which may occur through effects of the trait on the average fecundity (λ_n), the probability of survival of competing juveniles (s_c), and on the probability of the deme to resist environmental disturbances (s_d). Because niche expansion may affect all of these parameters (nonexclusively), our model retains the population sensitivity brought by niche expansion under a broad range of biological settings.

Likewise, helping will also be selected for under range expansion, because colonization of new territories prevents the benefits of helping from being eliminated by kin competition. Such a process can occur locally, by an expansion of the territory of the focal group so as to accommodate more adult individuals. Such a local boost in group size can be accounted for by the effect of helping on the survival probability of juveniles during competition (s_c), as considered in our model. But the process of group expansion can be facilitated by helping at a larger scale. For instance, the cooperative social system of invasive ant species (fire ant, *Solenopsis invicta*; Argentine ant, *Linepithema humile*) certainly played a role in enhancing their invasion. From our arguments, the very process of invasion and expanding dynamics is expected to reinforce in turn social integration, if the invasion dynamics follows a propagule pool model of colonization (the expansion of subpopulations in invading Argentine ant is primarily due to the local budding of new colonies from existing nests at the invasion front; Ingram and Gordon 2003). Among recent invaders, our own species is most noticeable. Demographic sensitivity certainly played a crucial role in our humans' evolutionary history, as shown by the dramatic increase in population size over recent times. According to our models, range expansion offered an opportunity for the evolution of kin-selected helping, which in practice also means warfare and ethnic replacements. Furthermore, as discussed above, warfare itself can be mimicked by an environmental disturbance rate to which the focal deme must resist, thereby creating ecological conditions favoring the evolution of helping.

That intergroup conflict is important for the evolution of helping in humans was already emphasized by Hamilton (1975) and has been reconsidered on the basis of simulations (Bowles et al. 2003; Boyd et al. 2003). In the setting of these latter works, stages of warfare occur in each time period between randomly paired groups. Then, the winning group,

the one with the largest number of helpers, replicates itself in the territory of the losing group. In our propagule model, a similar replication of groups occurs, but the process is more gradual as groups of helpers have only a higher probability of contributing the successful propagule.

Direct Versus Kin Versus Group Selection

Whether helping evolves by kin interactions or by direct benefits is a recurrent question (Clutton-Brock 2002). Kin interaction effects are sometimes considered negligible in many social groups because relatedness would be too low. In our models (and in nature), demography affects simultaneously the direct fitness effects and the kin interactions, so that the relative magnitude of each is not obvious a priori. However, our analytical formulation allows comparing kin-interaction effects with direct effects, which are obtained by replacing $Q_0^R(n)$ by $1/n$ in the formulae for S . One can thus evaluate the level of helping that would evolve by direct effects on fitness alone and compare to the level of helping that evolves when all fitness effects are taken into account. Hence, if altruism is defined from effects on fitness (as Hamilton [1964] defined it) rather than from effects on fecundity (as did Taylor 1992a), a helping act that results in a negative total direct effect can be interpreted as altruistic. Although we did not present such computations, we note that such altruism occurs in all our models under a range of parameter values, as it does in Taylor's original model (for the computation of fitness costs and benefits in the latter model see Rousset, p. 114). Our results thus suggest that group fission and demographic sensitiveness allow for the evolution a large spectrum of unconditional altruistic helping. The present analytical framework also emphasizes that, as in simpler models (Hamilton 1975), group selection (and in particular the S_{Pr} component) is a component of the kin selection process, rather than an alternative to it.

ACKNOWLEDGMENTS

We thank our colleagues for providing examples of cooperation and warfare within and between groups. LL and NP acknowledge financial support from the Fond National de la Recherche Scientifique. This is publication ISEM 06-034.

LITERATURE CITED

- Adams, E. S. 1990. Boundary disputes in the territorial ant *Azteca trigona* affects of asymmetries in colony size. *Anim. Behav.* 39: 321–328.
- Boesch, C. 2002. Cooperative hunting roles among tai chimpanzees. *Hum. Nat.* 13:27–46.
- Bowles, S., H. K. Choi, and A. Hopfensitz. 2003. The co-evolution of individual behaviors and social institutions. *J. Theor. Biol.* 223:135–147.
- Boyd, R., H. Gintis, S. Bowles, and P. J. Richerson. 2003. The evolution of altruistic punishment. *Proc. Natl. Acad. Sci. USA* 100:3531–3535.
- Breed, M. D., E. Guzman-Novoa, and G. J. Hunt. 2004. Defensive behavior of honey bees: organization, genetics and comparisons with other bees. *Annu. Rev. Entomol.* 49:271–298.
- Chapuisat, M., J. Goudet, and L. Keller. 1997. Microsatellites reveal high population viscosity and limited dispersal in the ant *Formica paralogubris*. *Evolution* 51:475–482.

- Clutton-Brock, T. H. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72.
- Comins, H. N., W. D. Hamilton, and R. M. May. 1980. Evolutionarily stable dispersal strategies. *J. Theor. Biol.* 82:205–230.
- Cooney, R. 2002. Colony defense in damaraland mole-rats *Cryptomys damarensis*. *Behav. Ecol.* 13:160–162.
- Creel, S., and N. M. Creel. 1995. Communal hunting and pack size in African wild dogs *Lycaon pictus*. *Anim. Behav.* 50:1325–1339.
- Duffy, J. E., C. L. Morrison, and K. S. Macdonald. 2002. Colony defense and behavioral differentiation in the eusocial shrimp *Synalpheus regalis*. *Behav. Ecol. Sociobiol.* 51:488–495.
- Engels, W., P. Rosenkranz, and E. Engels. 1995. Thermoregulation in the nest of the neotropical stingless bee *Scaptotrigona postica* and a hypothesis on the evolution of temperature homeostasis in highly eusocial bees. *Stud. Neotropical Fauna Environ.* 30(4):193–205.
- Fernandez-Escudero, I., P. Seppa, and P. Pamilo. 2001. Dependent colony founding in the ant *Proformica longiseta*. *Insectes Soc.* 48:80–82.
- Fix, A. G. 1979. Anthropological genetics of small populations. *Annu. Rev. Anthropol.* 8:207–230.
- Fournier, D., S. Aron, and M. C. Milinkovitch. 2002. Investigation of the population genetic structure and mating system in the ant *Pheidole pallidula*. *Mol. Ecol.* 11:1805–1814.
- Gandon, S., and Y. Michalakis. 1999. Evolutionary stable dispersal rate in a metapopulation with extinction and kin competition. *J. Theor. Biol.* 199:275–290.
- Giraud, T., R. Blatrix, C. Poteaux, M. Solignac, and P. Jaisson. 2000. Population structure and mating biology of the polygynous ponerine ant *Gnamptogenys striatula* in Brazil. *Mol. Ecol.* 9:1835–1841.
- Gompper, M. E., J. L. Gittleman, and R. K. Wayne. 1998. Dispersal, philopatry, and genetic relatedness in a social carnivore: comparing males and females. *Mol. Ecol.* 7:157–163.
- Grinstead, C. M., and J. L. Snell. 1997. Introduction to probability. 2nd ed. American Mathematical Society, Providence, RI.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour. I and II. *J. Theor. Biol.* 7:1–52.
- . 1975. Innate social aptitudes in man, an approach from evolutionary genetics. Pp. 133–157 in R. Fox, ed. *Biosocial anthropology*. Malaby Press, London.
- Ingram, K. K., and D. M. Gordon. 2003. Genetic analysis of dispersal dynamics in an invading population of argentine ants. *Ecology* 84:2832–2842.
- Kays, R. W., and J. L. Gittleman. 2001. The social organization of the kinkajou *Potos flavus* (Procyonidae). *J. Zool.* 253:491–504.
- Kutsukake, M., H. Shiba, N. Nikoh, M. Morioka, T. Tamura, T. Hoshino, S. Ohgiya, and T. Fukatsu. 2004. Venomous protease of aphid soldier for colony defense. *Proc. Natl. Acad. Sci. USA* 101:11338–11343.
- Lefebvre, D., N. Ménard, and J. S. Pierre. 2003. Modelling the influence of demographic parameters on group structure in social species with dispersal asymmetry and group fission. *Behav. Ecol. Sociobiol.* 53:402–410.
- Le Galliard, J., R. Ferrière, and U. Dieckmann. 2003. The adaptive dynamics of altruism in spatially heterogeneous populations. *Evolution* 57:1–17.
- Mabelis, A. A. 1979. Relationship between aggression and predation in the wood ant (*Formica polyctena* Forst.). *Neth. J. Zool.* 29:451–462.
- Mitteldorf, J., and D. Wilson. 2000. Population viscosity and the evolution of altruism. *J. Theor. Biol.* 204:481–496.
- Okamoto, K., and S. Matsumura. 2001. Group fission in moor macaques (*Macaca maurus*). *Int. J. Primatol.* 22:481–493.
- Peeters, C., and F. Ito. 2001. Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annu. Rev. Entomol.* 46:601–630.
- Perrin, N., and L. Lehmann. 2001. Is sociality driven by the costs of dispersal or the benefits of philopatry? A role for kin discrimination mechanisms. *Am. Nat.* 158:471–483.
- Rousset, F. 2004. Genetic structure and selection in subdivided populations. Princeton Univ. Press, Princeton, NJ.
- Rousset, F., and S. Billiard. 2000. A theoretical basis for measures of kin-selection in subdivided populations: finite populations and localized dispersal. *J. Evol. Biol.* 2000:824–825.
- Rousset, F., and O. Ronce. 2004. Inclusive fitness for traits affecting metapopulation demography. *Theor. Popul. Biol.* 142:1357–1362.
- Scheffrahn, W., N. Menard, D. Vallet, and B. Gaci. 1993. Ecology, demography, and population-genetics of Barbary macaques in Algeria. *Primates* 34(3):381–394.
- Schweitzer, P. J. 1968. Perturbation theory and finite markov chains. *J. Appl. Probability* 5:401–413.
- Seppä, P., and P. Pamilo. 1995. Gene flow and population viscosity in *Myrmica* ants. *Heredity* 74:200–209.
- Slatkin, W. D. 1977. Gene flow and genetic drift in a species subject to frequent local extinctions. *Theor. Popul. Biol.* 12:253–262.
- Stander, P. E. 1992. Cooperative hunting in lions: the role of the individual. *Behav. Ecol. Sociobiol.* 29:445–454.
- Stanford, C. B. 1995. The influence of chimpanzee predation on group-size and antipredator behavior in red colobus monkeys. *Anim. Behav.* 49:577–587.
- Starks, P. T., and D. C. Gilley. 1999. Heat shielding: a novel method of colonial thermoregulation in honey bees. *Naturwissenschaften* 86(9):438–440.
- Starks, P. T., R. N. Johnson, A. J. Siegel, and M. M. Decelle. 2005. Heat shielding: a task for youngsters. *Behav. Ecol.* 16:128–132.
- Taylor, P. D. 1992a. Altruism in viscous populations: an inclusive fitness model. *Evol. Ecol.* 6:352–356.
- . 1992b. Inclusive fitness in a homogeneous environment. *Proc. R. Soc. Lond. B* 240:299–302.
- Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. *J. Theor. Biol.* 54:1135–1141.
- Taylor, P. D., and A. J. Irwin. 2000. Overlapping generations can promote altruistic behavior. *Evolution* 54:27–37.
- Tello, N. S., M. Huck, and E. W. Heymann. 2002. Boa constrictor attack and successful group defence in moustached tamarins, *Saguinus mystax*. *Folia Primatol.* 73:146–148.
- Van Baalen, M., and A. Rand. 1998. The unit of selection in viscous populations and the evolution of altruism. *J. Theor. Biol.* 193:631–648.
- Waterman, J. M. 2002. Delayed maturity, group fission and the limits of group size in female cape ground squirrels (Sciuridae: *Xerus inauris*). *J. Zool.* 256:113–120.
- Wilson, M. L., N. F. Britton, and N. R. Franks. 2002. Chimpanzees and the mathematics of battle. *Proc. R. Soc. Lond. B* 269:1107–1112.
- Wrangham, R. W. 1999. Evolution of coalitionary killing. *Yearb. Phys. Anthropol.* 42:1–30.

Corresponding Editor: T. Day

APPENDIX 1: ENVIRONMENTAL STOCHASTICITY

Competition between Propagules during Recolonization

From the definition of S (eq. 2) and the fitness function (eq. 4), when $z_{\bullet} = z_{\text{B}}^{\text{B}} = z_1 = 0$, S takes the form

$$S = -C + [B - (B - C)(1 - m)^2 s_d] Q_{\text{B}}^{\text{B}} + D s_d Q_{\text{B}}^{\text{B}}, \quad (\text{A1})$$

where Q_{B}^{B} is the relatedness of two homologous genes sampled with replacement. This coefficient of relatedness can be written as

$$Q_{\text{B}}^{\text{B}} = \frac{1}{N_{\text{max}}} + \left(\frac{N_{\text{max}} - 1}{N_{\text{max}}} \right) Q_{\text{B}}^{\text{D}}, \quad (\text{A2})$$

where Q_{B}^{D} is the relatedness of two homologous genes sampled without replacement. In the infinite island model of dispersal, they are related by the following recursion at equilibrium:

$$Q_{\text{B}}^{\text{D}} = (1 - m)^2 s_d Q_{\text{B}}^{\text{D}} + (1 - s_d) \phi Q_{\text{B}}^{\text{D}}, \quad (\text{A3})$$

where s_d denotes the probability of deme survival and ϕ is the probability that two recolonizers come from the same deme. Solving the last two equations yields

$$Q_{\text{B}}^{\text{D}} = \frac{1}{1 + [\phi(1 - s_d) + 1 - (1 - m)^2 s_d](N_{\text{max}} - 1)}. \quad (\text{A4})$$

From this and from equation (A1) one can obtain an expression for S in terms of basic parameters of the model (eq. 5). Alternatively, when the probability of common origin of two colonizers is set to zero ($\phi = 0$), we can use equation (A3) to simplify equation (A1) to: $S = -C + BQ_0^R - (B - C)Q_0^D + Ds_d Q_0^R$. Then using (A2) yields:

$$S = (B/N_{\max} - C)(1 - Q_0^D) + Ds_d Q_0^R. \quad (\text{A5})$$

Competition between Individuals during Recolonization

During recolonization of extinct demes, competition can also occur between individuals for access to breeding spots instead of occurring between propagules for access to demes. In this situation, the inclusive fitness effect of helping is still obtained from S (eq. 2) but with the fitness function taking the more general form given by equation (A7) below. This form allows us to evaluate the fitness effect under different assumptions about the life cycle when only environmental stochasticity occurs. If individuals disperse independently rather than through propagules, for any parent the expected number of dispersing offspring that reach adulthood depends on the probability ϕ of common origin of two of these offspring. That is, the expected number of dispersing offspring of the focal individual reaching adulthood in an extinct deme is $w_d(0, N_{\max}, N_{\max}) \equiv b_{\bullet}/[\sigma(z_0^R)\phi b_{\bullet} + \sigma(z_1)(1 - \phi)b_d]$ and the number of these offspring reaching adulthood in a nonextinct deme is $w_d(N_{\max}, N_{\max}, N_{\max}) \equiv db_{\bullet}/\{(1 - d)b_d + d[\sigma(z_0^R)\phi b_{\bullet} + \sigma(z_1)(1 - \phi)b_d]\}$. By contrast, the focal individual number of offspring reaching adulthood in the focal deme is $w_p(N_{\max}, N_{\max}) \equiv (1 - d)b_{\bullet}/[(1 - d)b_R + db_d]$ which is the same as under the model competition between propagules. Assuming no effect of helping on the survival probability of demes ($D = 0$), the inclusive fitness effect reduce to

$$S = (B/N_{\max} - C)(1 - Q_0^D). \quad (\text{A6})$$

APPENDIX 2: DEMOGRAPHIC STOCHASTICITY

Fitness and Frequency Functions

In the presence of demographic stochasticity, fitness effects depend on the number of parents in a deme, and the reproductive value of offspring depend on the number of offspring settling in the deme. Then, we need to consider fitness functions conditional on such numbers. Thus we consider $w_p(n, n')$ which describes for a parent its expected number of offspring reaching adulthood in the deme of this parent, this number being considered conditional on the size n' of the deme in the offspring generation and on its size n in the parental generation. Likewise we consider $w_p(n, n', l)$ which describes for a parent its expected number of immigrant adult offspring, in demes of size n' in the offspring generation that were of size n in the parental generation, of an individual breeding in a deme of size l . As a simple example, in the model with environmental stochasticity alone, the fitness function equation (4) could have been written as

$$w = \sigma(z_0^R)w_p(N_{\max}, N_{\max}) + \sigma(z_1)[1 - \sigma(z_1)]w_d(0, N_{\max}, N_{\max}) + \sigma(z_0^R)\sigma(z_1)w_d(N_{\max}, N_{\max}, N_{\max}). \quad (\text{A7})$$

In this situation, the metapopulation consists of only two classes of demes, those that are extinct (size 0) and those that are at the ceiling patch size (size N_{\max}).

More generally, when demes can take various sizes and the average size of a deme is N_{eq} , it is convenient to further consider the frequency functions $f_p(n, n') \equiv w_p(n, n')/n'$ and $f_d(n, n', l) \equiv w_p(n, n', l)/n'$:

$$f_p(n, n') = f_p(n) \equiv \frac{n(1 - d)b_{\bullet}}{n(1 - d)b_R + N_{\text{eq}}db_d}, \quad (\text{A8})$$

which is the probability that a gene sampled in the focal deme of size n' in the offspring generation descend from the focal deme that was of size n in the parental generation and

$$f_d(n, n', l) = f_d(n, l) = \frac{l db_{\bullet}}{[n(1 - d) + N_{\text{eq}}d]b_d}, \quad (\text{A9})$$

which is the probability that a gene, conditional on its parental

deme being of size l , is sampled presently in a deme of size n' that was of size n in the parental generation. These functions are independent of n' , a result which follows from the assumptions that the fecundity of each individual in the metapopulation is independently Poisson-distributed, that each juvenile disperses independently, and that the density-dependent survival probability of each juvenile is independent of that of the other juveniles (Rousset and Ronce 2004). According to such assumptions, and given there were n parents in a deme, the number of juveniles g that are competing for this deme after dispersal follows the Poisson distribution $P(g; \lambda_n)$ with mean

$$\lambda_n = n(1 - d)b_R + N_{\text{eq}}db_d. \quad (\text{A10})$$

Then the probability that a number j of juveniles survives density-dependent competition in a deme that was of size n in the parental generation can be written

$$\Pr(J = j | n) = \sum_{g=0}^{\infty} B[j; g, s_c(g)]P(g; \lambda_n), \quad (\text{A11})$$

where $B[j; g, s_c(g)]$ is the binomial term giving the number j of juveniles surviving competition as function of the number g of juveniles that come in competition and of their individual survival probability $s_c(g)$. Individual density-dependent survival probability as a function of trait value is given by

$$s_c(g) = s_s g^{a_s} e^{-k_s(1 - D z_0^R)(g-1)}. \quad (\text{A12})$$

Since the maximum size of a deme is set to N_{\max} , the probability of the transition of the focal deme of size n in the parental generation to a deme of size n' in the offspring generation is given by:

$$\Pr(n' | n) = \begin{cases} [1 - \sigma(z_0^R)] + \sigma(z_0^R)\Pr(J = 0 | n) & \text{for } n' = 0 \\ \sigma(z_0^R)\Pr(J = n' | n) & \text{for } N_{\max} > n' > 0 \\ \sigma(z_0^R)\Pr(J \geq N_{\max} | n) & \text{for } n' = N_{\max}. \end{cases} \quad (\text{A13})$$

Measure of Selection S

The inclusive fitness effect S is expressed in terms of the following variables. It involves the backward transition probability $\Pr(n | n') = \Pr(n' | n)\Pr(n)/\Pr(n')$ that a deme of size n' derives from a deme of size n , where $\Pr(n' | n)$ is the forward transition probability of a deme of size n to a deme of size n' given above. The stationary probabilities that a deme will be of size n are solutions of the recursions:

$$\Pr(n') = \sum_{n=0}^{N_{\max}} \Pr(n' | n)\Pr(n). \quad (\text{A14})$$

As for constant deme size, we need the probabilities of identity $Q_0(n)$ of two homologous genes sampled within a deme, here conditional on deme size, sampled either with $[Q_0^R(n)]$ or without $[Q_0^D(n)]$ replacement. They are solutions of

$$Q_0^R(n) = \frac{1}{n} + \left(\frac{n-1}{n}\right)Q_0^R(n) \quad (\text{A15})$$

and

$$Q_0^D(n') = \sum_{n=0}^{N_{\max}} \Pr(n | n')f_p(n)^2 Q_0^R(n), \quad (\text{A16})$$

(Rousset and Ronce 2004, eq. 29). Finally, we need the relative reproductive value $v(n)$ of a deme of size n (here the relative reproductive value of all individuals in a focal deme), which are solutions of the recursions:

$$v(n) = \sum_{n'=0}^{N_{\max}} \left[f_p(n)\Pr(n' | n) + \sum_{l=0}^{N_{\max}} f_d(l, n)\Pr(n' | l)\Pr(l) \right] v(n'). \quad (\text{A17})$$

Notice that $v(n) \equiv \alpha(n)/\Pr(n)$, where $\alpha(n)$ is the reproductive value of all demes of size n given in Rousset and Ronce (2004).

Then the measure of selection takes the form $S = S_f + S_{Pr}$, where

$$S_f = \sum_{n'=0}^{N_{\max}} \sum_{n=0}^{N_{\max}} v(n') \Pr(n' | n) \times \left\{ \frac{\partial f_p(n)}{\partial z_{\bullet}} + \frac{\partial f_p(n)}{\partial z_0^R} Q_0^R(n) + \sum_{l=0}^{N_{\max}} \Pr(l) \left[\frac{\partial f_d(n, l)}{\partial z_{\bullet}} + \frac{\partial f_d(n, l)}{\partial z_0^R} Q_0^R(l) \right] \right\} \Pr(n) \quad (\text{A18})$$

and

$$S_{Pr} = \sum_{n'=0}^{N_{\max}} \sum_{n=0}^{N_{\max}} v(n') \frac{\partial \Pr(n' | n)}{\partial z_0^R} f_p(n) Q_0^R(n) \Pr(n). \quad (\text{A19})$$

Effect on S_f , the Relative Contribution for Given Offspring Deme Size

We now evaluate S_f in $z_{\bullet} = z^R = z_1 = 0$ and simplify using $N_{eq} = \sum_l l \Pr(l)$. This yields:

$$S_f = \sum_{n'=0}^{N_{\max}} \sum_{n=0}^{N_{\max}} v(n') \Pr(n' | n) \Pr(n) \times \left\{ -C - (B - C) f_p(n')^2 Q_0^R(n) + B \left[f_p(n) Q_0^R(n) + \sum_{l=0}^{N_{\max}} f_d(n, l) \Pr(l) Q_0^R(l) \right] \right\}, \quad (\text{A20})$$

The total coefficients of $(B - C)$ for each value of n' can be simplified using equation (A16) and $v(n') = \alpha(n')/\Pr(n')$, and the whole term in braces can be simplified using equation (A17) for each value of n . This yields:

$$S_f = \sum_{n=0}^{N_{\max}} \alpha(n) [-C - (B - C) Q_0^D(n) + B Q_0^R(n)] = \sum_{n=0}^{N_{\max}} \alpha(n) (B/N - C) [1 - Q_0^D(n)] \quad (\text{A21})$$

from equation (A15).

Effect on Focal Deme Size

From equation (A11), the change in the transition probability of deme size is

$$\frac{\partial \Pr(n' | n)}{\partial z_0^R} = \sum_{g=0}^{\infty} \left\{ \frac{\partial s_c(g)}{\partial z_0^R} \frac{[n' - g s_c(g)]}{s_c(g) [1 - s_c(g)]} + \frac{\partial \ln(\lambda_n)}{\partial z_0^R} (g - \lambda_n) \right\} \times B[j; g, s_c(g)] P(g; \lambda_n). \quad (\text{A22})$$

In this expression we have considered effects of the behavior on the mean number of juveniles competing in the focal deme (λ_n) and on the probability of survival during competition [$s_c(g)$]. We did not find any simple form of S_{Pr} from this expression. Nevertheless, interpretations in term of reproductive values can be derived in the case where helping has no effect on juvenile survival during competition ($\partial s_c(g)/\partial z_0^R = 0$). We first consider the case where density-dependent regulation occurs only through random culling of juveniles when the number of competing offspring exceeds the ceiling number N_{\max} . Note first that from equation (A13) we have for all $n' < N_{\max}$:

$$\frac{\partial \Pr(n' | n)}{\partial z_0^R} = \frac{\partial \lambda_n (n' - \lambda_n)}{\partial z_0^R \lambda_n} \Pr(n' | n) = \frac{\partial \ln(\lambda_n)}{\partial z_0^R} (n' - \lambda_n) \Pr(n' | n) \quad \text{and} \quad (\text{A23})$$

$$\begin{aligned} \frac{\partial \Pr(N_{\max} | n)}{\partial z_0^R} &= - \sum_{n' < N_{\max}} \frac{\partial \Pr(n' | n)}{\partial z_0^R} \\ &= \frac{\partial \ln(\lambda_n)}{\partial z_0^R} \sum_{n' < N_{\max}} (\lambda_n - n') \Pr(n' | n) \\ &= \frac{\partial \ln(\lambda_n)}{\partial z_0^R} [\lambda_n - E(n' | n) - (\lambda_n - N_{\max}) \Pr(N_{\max} | n)]. \end{aligned} \quad (\text{A24})$$

This is of the same form as equation (A23), except for the additional term $\lambda_n - E(n' | n)$, which is the reduction of deme size through pure ceiling regulation since λ_n is the expected number of competing juveniles. Then

$$S_{Pr} = \sum_{n=0}^{N_{\max}} f_p(n) \frac{\partial \ln(\lambda_n)}{\partial z_0^R} Q_0^R(n) \Pr(n) \times \left\{ v(N_{\max}) [\lambda_n - E(n' | n)] + \sum_{n'=0}^{N_{\max}} v(n') (n' - \lambda_n) \Pr(n' | n) \right\}. \quad (\text{A25})$$

Let us expand the inner sum as

$$\sum_{n'=0}^{N_{\max}} v(n') [n' - E(n' | n) + E(n' | n) - \lambda_n] \Pr(n' | n). \quad (\text{A26})$$

Here $\sum_{n'=0}^{N_{\max}} v(n') \{n' - E[n' | n]\} \Pr(n' | n)$ is in the form $E(XY) = E(X)E(Y) + \text{Cov}(XY)$ where in addition $E(Y) = E\{(n' - E(n' | n))\} = 0$. Hence the inner sum is

$$\text{Cov}[v(n'), n' | n] + [E(n' | n) - \lambda_n] E[v(n') | n] \quad (\text{A27})$$

and the whole expression in braces in equation (A25) is

$$\text{Cov}[v(n'), n' | n] + [\lambda_n - E(n' | n)] \{v(N_{\max}) - E[v(n') | n]\}. \quad (\text{A28})$$

Thus, S_{Pr} is a weighted sum of such terms. Although a proof seems difficult to obtain and exceptions might turn out, it appears to be generally positive, because the deme reproductive value is generally positively correlated with its size (thus $\text{Cov}[v(n'), n' | n] > 0$ and $v(N_{\max}) - E[v(n') | n] > 0$), and the reduction in deme size due to culling ($\lambda_n - E[n' | n]$) is necessarily positive.

Now we assume that the survival probability $s_c(g)$ of juveniles can take any shape of density dependence (but is still independent of helping). We evaluate S_{Pr} in the same way as above and the simplification produces a result similar in form to equation (A25) but more cumbersome to derive. The whole expression in the curly braces of equation (A25) then reads

$$\begin{aligned} &\text{Cov}[v(n'), n' | n] \\ &+ E\{[\lambda_n - E(n' | n) - E(g | n', n) + n'] [v(N_{\max}) - v(n')] | n\}, \end{aligned} \quad (\text{A29})$$

where $E(g | n', n)$ is the expected number of juveniles in a deme after dispersal conditional on both the parental generation being of size n and the descendant generation being of size n' . The outward expectation is over all values of g and n' . The term $\lambda_n - E(n' | n)$ is as before the average reduction in deme size through competition between juveniles after dispersal. However, beyond this term common to all values of n' in the outward expectation, there is an additional term $E(g | n', n) - n'$ which differs for each value of n' , and which is the reduction through competition, conditional on the final deme size n' . So, the first factor of the outward expectation

is the difference between the unconditional reduction in deme size and the reduction conditional on n' . Here, regulation is mainly determined by the values of the parameters of equation (A12). Thus, it is not formally necessary to impose a ceiling deme size (N_{\max}) to prevent a blow up of deme size. We can formally let $N_{\max} \rightarrow \infty$, in which case $E(g | n', n) \rightarrow \lambda_n$ and $v(N_{\max}) \rightarrow 0$, and equation (A29) reduces to

$$\text{Cov}[v(n'), n' | n] + E\{[E(n' | n) - n']v(n') | n\}. \tag{A30}$$

APPENDIX 3: COMPUTING POPULATION SENSITIVITY

Our aim here is to provide a convenient formula for evaluating demographic sensitivity to change in resident trait value, that is to the change dN_{eq}/dz in average deme size resulting from a change in the behavior of all the individuals in the population. Our approach holds whenever deme size follows a Markov chain with a single irreducible set of states, whose one-step transition probabilities $\text{Pr}(n' | n)$ are written as functions of current resident trait value z and of average deme size N_{eq} (itself a function of z in earlier generations).

We denote \mathbf{p} the stationary distribution of the Markov chain. Then $dN_{\text{eq}}/dz = \mathbf{n} \cdot d\mathbf{p}/dz$ where $\mathbf{n} \equiv (0, 1, \dots, N_{\max})$ is the vector of deme sizes. Let \mathbf{P} be the unperturbed transition matrix, with stationary distribution \mathbf{p}° . Following Schweitzer (1968), the perturbation of \mathbf{p}° resulting from a perturbation of \mathbf{P} can be computed conveniently as

$$\Delta \mathbf{p} = \mathbf{Z} \Delta \mathbf{P} \mathbf{p}^\circ + O(\Delta \mathbf{P}^2), \tag{A31}$$

where

$$\mathbf{Z} \equiv (\mathbf{I} - \mathbf{P} + \mathbf{P}_c)^{-1} \tag{A32}$$

is the so-called fundamental matrix of the Markov chain (Grinstead and Snell 1997, p. 456). Here the matrix \mathbf{P}_c is the matrix that each row is the vector \mathbf{p}° , and \mathbf{I} is the identity matrix.

From the above we need to know the perturbation $\Delta \mathbf{P}$ due to a perturbation Δz of resident trait value. The total effect $\Delta \mathbf{P}$ is the sum of effects through the changes $\partial \mathbf{P}(z, N_{\text{eq}})/\partial z$ in transition probabilities for N_{eq} fixed and through the changes $\partial \mathbf{P}(z, N_{\text{eq}})/\partial N_{\text{eq}}$ in transition probabilities due to variation in N_{eq} :

$$\Delta \mathbf{P} = \Delta z \frac{\partial \mathbf{P}}{\partial z} + \Delta N_{\text{eq}} \frac{\partial \mathbf{P}}{\partial N_{\text{eq}}} + \text{higher order terms}. \tag{A33}$$

We plug this into equation (A31), premultiply by \mathbf{n} and solve for dN_{eq}/dz :

$$\frac{dN_{\text{eq}}}{dz} = \frac{\mathbf{n} \cdot \mathbf{Z} \frac{\partial \mathbf{P}}{\partial z} \mathbf{p}^\circ}{1 - \mathbf{n} \cdot \mathbf{Z} \frac{\partial \mathbf{P}}{\partial N_{\text{eq}}} \mathbf{p}^\circ}. \tag{A34}$$

This derivative is by definition taken in a metapopulation with a monomorphic resident phenotype z .