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E-Article

From Infanticide to Parental Care: Why Spatial Structure Can Help Adults Be Good Parents

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abstract: We investigate the evolution of parental care and cannibalism in a spatially structured population where adults can either help or kill juveniles in their neighborhood. We show that spatial structure can reverse the selective pressures on adult behavior, leading to the evolution of parental care, whereas the nonspatial model predicts that cannibalism is the sole evolutionary outcome. Our analysis emphasizes that evolution of such spatially structured populations is best understood at the level of the cluster of invading mutants, and we define invasion fitness as the growth rate of that cluster. We derive an analytical expression for the selective pressures on the trait and show that relatedness and Hamilton's rule are recovered as emergent properties of the spatial ecological dynamics. When adults can also help other adults, the benefits to each class of recipients are weighted by the class reproductive value, a result consistent with that of other models of kin selection. Finally, we advocate a different approach to moment equations and argue that even though the development of moment closure approximations is a necessary line of research, much-needed ecological and evolutionary insight can be gained by studying the unclosed moment equations.

Keywords: altruism, moment equations, invasion fitness, age structure, cannibalism, kin selection.

Parental care is a particular form of altruism where an individual conveys benefits to its offspring at a cost to itself. Explaining how such a behavior can evolve therefore runs up against the fundamental puzzle of altruism: because it does not pay to behave altruistically in a selfish population, one can expect that altruism cannot evolve in the absence of mechanisms counterbalancing the fitness cost of altruism. Kin selection has been argued to be one of the main forces driving the evolution of parental care: parents that help their offspring have an indirect fitness benefit because parent and offspring are related. As Hamilton (1964, p. 2) argued in his seminal paper, "there is nothing special about the parent-offspring relationship except its close degree and a certain fundamental asymmetry." Indeed, parental care is just a special form of cooperation and a special case of the general theory of kin selection. The fact that there is "nothing special about the parent-offspring relationship" can be more clearly seen if one considers the alternative behavior of infanticide or cannibalism. In some cases, it can pay more to a parent to kill or eat its offspring than to provide them with care (Polis 1981).

Parental care and cannibalism are opposite but widespread behaviors. Whereas studies of the evolution of parental care abound, mainly in relation to sexual selection theory and parent-offspring conflict (Clutton-Brock 1991), the evolution of cannibalism has received less attention, perhaps because it has long been considered an abnormal behavior. Nevertheless, there is now a large body of evidence showing that adaptive cannibalism occurs in a wide range of taxa, from ciliates to vertebrates. Current predictions and evidence suggest that cannibalism should be favored under conditions of high population density, food shortage, and increased competition for resources (Polis 1981; van den Bosch et al. 1988; Elgar and Crespi 1992) or an increase of the cost-to-benefit ratio of parental care (Manica 2004). Often, cannibalism is an asymmetric interaction (typically, adults eating juveniles), where, according to kin selection theory, the main cost for the cannibal should be the risk of eating a relative. Despite this, filial (or sibling) cannibalism is common, especially in fish (Manica 2002).

It is often thought that mechanisms of recognition or discrimination of related individuals are required for kin

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selection to opeate (see, e.g., Pfennig 1997). Although parental care is usually directed toward related individuals (Waldman 1988; Clutton-Brock 1991), examples of indiscriminate care exist, for instance, communal nursing in mammals (Hoogland et al. 1989) and communal breeding in birds (Brown 1987). Besides, parental care in many noncolonial birds involves indirect recognition through spatial cues, and those birds treat any young in their nest as offspring (Beecher et al. 1981), which creates opportunities for brood parasites (Rohwer and Freeman 1989). Examples also exist in other species, such as ground squirrels (Holmes and Sherman 1982) and beetles (Müller et al. 1990).

Also as expected, cannibalism is generally directed away from relatives (for reviews and also for examples of kin-biased cannibalism, see Elgar and Crespi 1992; Pfennig 1997), but several studies have given evidence of indiscriminate cannibalism, including egg cannibalism by hatchling snails (Baur 1987) and by nestmate ant queens (Bourke 1994), larval cannibalism in the Indian meal moth (Boots 2000) and in tree-hole mosquitoes (Sherratt et al. 1999), filial cannibalism in four species of fish (DeWoody et al. 2001; Bandoli 2006), cannibalism in poison frogs (Summers and Symula 2001), and occasionally pup cannibalism in rodents (Elwood and Ostermeyer 1984; Hoogland 1985).

These findings do not imply that kin selection is unable to explain such behaviors. Hamilton's (1964) derivation makes it clear that an altruistic behavior (e.g., parental care) will be selected if one meets, on average, sufficiently many related individuals without having to discriminate between kin and nonkin (Mateo 2004; van Baalen and Jansen 2006). Limited dispersal is one of the ecological mechanisms that can lead to individuals having a higher probability of meeting kin than nonkin.

Hamilton (1964) coined the term "viscous population" to refer to populations with low dispersal. He conjectured that in such viscous populations, altruism should be favored because individuals tend to be surrounded by relatives. This has led to a wealth of theoretical studies on spatial models of cooperation. Hamilton's conjecture was at first dismissed by patch models in which increased local competition caused by population viscosity could cancel the benefits of local altruistic interactions (Taylor 1992*a*; Wilson et al. 1992; Queller 1994). These models assume that local population regulation is inelastic (Taylor 1992*b*), with fixed patch density, so that groups (patches) containing more altruists suffer from increased competition. This has led to the idea that for altruism to be favored, competition must take place at a more global scale than altruistic interactions (Kelly 1992, 1994; West et al. 2002). At the same time, Matsuda et al. (1992), Harada et al. (1995), and Nakamaru et al. (1997) have shown that altruists and nonaltruists can coexist in a viscous population but not when the population is well mixed. In these models, space is modeled as a network of sites where altruistic interactions and competition for space both take place locally. Building on these models, van Baalen and Rand (1998) have shown that the invasion condition of altruists can be interpreted as an emergent Hamilton's rule. Le Galliard et al. (2003, 2005) have further studied the interplay of altruism and mobility and have shown that low habitat saturation could cause kin competition to become negligible. Despite the variety of approaches, we begin to have a clearer theoretical picture of how spatial structure affects both kin selection and kin competition, and the general conclusion is that spatial structure can provide a subtle yet decisive advantage to cooperation (but see Hauert and Doebeli 2004 for a discussion).

The role of spatial self-structuring as a template for evolution has drawn much attention during the past 20 years (Boerlijst et al. 1993; Keeling and Rand 1995; Rand et al. 1995; Read and Keeling 2002). Spatial structure is an important component of the feedback loop between ecological and evolutionary dynamics: the evolution of a given trait shapes the local structure of the population, which in turn creates new selective pressures acting on the evolving trait (Le Galliard et al. 2005; Lion et al. 2006). As a consequence, the evolution of spatially structured populations often displays features different from the evolution of well-mixed populations. For instance, parasite virulence and transmission have been shown to evolve toward lower levels in viscous populations (Boots and Sasaki 1999; Read and Keeling 2002; van Baalen 2002); the potential for evolutionary branching can be reduced (Mágori et al. 2005), and, as discussed above, cooperation is generally favored in viscous populations.

A novel aspect of this work is that we extend previous analyses of the evolution of cooperation in spatially structured populations by incorporating a stage structure. In our model, adults can either help or kill juveniles depending on the value of a continuous trait, and we examine whether population viscosity can favor the evolution of care from adults to juvenile, as can be expected from previous spatial models of cooperation. We recover a spatial version of Hamilton's rule and show that spatial clustering can provide an explanation for the origin of parental care in the absence of kin recognition. We discuss the conceptual implications and limitations of these results and refer the reader to a companion article (S. Lion and M. van Baalen, unpublished manuscript) for more technical issues. Finally, we advocate the use of correlation equations (Matsuda et al. 1992; Rand 1999) as a useful analytical tool to get qualitative insight into the evolution of spatially structured populations.

Evolution of a Stage-Structured Viscous Population

The Model

We consider a population of juveniles (J) and adults (A) living on an (infinite) network of sites. Each site can be empty (o) or occupied by one individual. Juveniles become adults at a constant maturation rate μ. Adults reproduce clonally at rate b_A to an empty neighboring site. Reproduction is therefore density dependent. Juveniles and adults have background mortality rates d_J and d_A, respectively (fig. 1). Mobility of juveniles and adults is also included in our framework, but we shall not address the effect of dispersal until later in the article.

We assume that adults can either increase or decrease the mortality rate of neighboring juveniles, depending on the value of a continuous trait c that can be negative (infanticide or cannibalism) or positive (care). We also make the assumption that adults cannot discriminate their kin and discuss later how kin discrimination could affect our conclusions.

The average death rate of a juvenile individual will then be

$$\delta_J = d_J - \beta c q_{A/J}, \tag{1}$$

where β is the conversion efficiency of adult behavior into juvenile survival and $q_{A/J}$ denotes the local density of adults around a juvenile, that is, the probability of finding an adult in the neighborhood of an average juvenile. Also, for the sake of simplicity, we assume a linear relationship between the trait and the phenotypic effect, but the whole analysis can be readily extended to general functional forms $\beta(c)$.

We further assume a trade-off between the trait c and adult reproduction b_A. Because adults will pay the cost or gain a benefit from their behavior only if there is a juvenile in their neighborhood, the birth rate of an adult will depend on the local density of juveniles. In appendix A, we show that the average birth rate takes the form

$$b_A = b_0 - \gamma(c)\frac{n-1}{n}q_{J/Ao}, \tag{2}$$

where n is the number of nearest neighbors, $q_{J/Ao}$ denotes the local density of juveniles around an adult that has at least one empty site in its neighborhood, and $\gamma(c)$ and c have the same sign, so that adult reproduction is decreased by care and increased by cannibalism. The factor $(n-1)/n$ reflects the fact that a successfully reproducing adult has at least one empty site among its neighbors and therefore cannot receive more than $(n-1)/n$ interactions with surrounding juveniles.

Table 1 lists the symbols used in the model, and appendix A gives a method to derive the expressions of δ_J and b_A. Note that b_A and $\delta_J > 0$, which sets an upper limit to the allowed value of c.

Spatial versus Nonspatial Evolutionary Dynamics

The nonspatial counterpart of this model assumes that adults can interact with any juvenile in the population, instead of interacting only with juveniles in their neighborhood, and can deposit an offspring in a randomly chosen empty site. Thus, local densities in equations (1) and (2) are replaced with the global densities p_A and p_J, respectively.

In order to show how such different assumptions on the scale of the interactions can affect the selective pressures on adult behavior, we performed stochastic simulations of both the spatial and the nonspatial version of the model. We use a probabilistic cellular automaton (Durrett and Levin 1994*a*, 1994*b*) with asynchronous updating on a triangular lattice with periodic boundary conditions (each site has six neighbors) and assume that if it starts

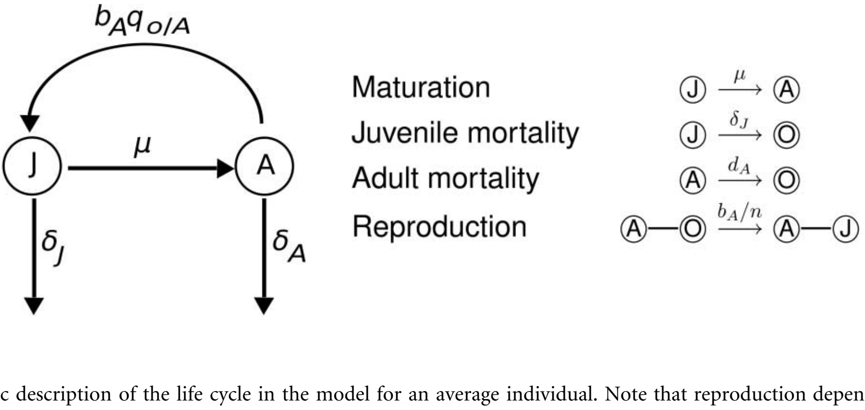

Figure 1: *Left*, schematic description of the life cycle in the model for an average individual. Note that reproduction depends on the availability of empty sites around an adult. *Right*, corresponding rules for the updating of the probabilistic cellular automaton.

Table 1: Table of parameters and variables

Type and symbol	Description
Space:	
n	Number of nearest neighbors
Demography:	
b_A	Birth rate of adult A
b_0	Background reproduction rate of adults
d_J	Background mortality rate of juveniles
d_A	Background mortality rate of adults
μ	Maturation rate
c	Resident altruistic or cannibalistic trait
c'	Mutant altruistic or cannibalistic trait
β	Conversion efficiency of adult behavior into juvenile survival
δ_J	Mortality rate of juveniles
$\gamma(c)$	Trade-off function between trait and reproduction
Variables:	
p_x	Global density of type x
$q_{i/j}$	Local density of type i as seen by type j ($0 \leq q_{i/j} \leq 1$)
$q_{i/jk}$	Local density of type i as seen by j individuals that have a k neighbor ($0 \leq q_{i/jk} \leq 1$)

from a population with zero investment, the trait c can evolve through rare mutation events with a small mutation step Δc (e.g., reproduction is unfaithful with a small probability, and when that occurs, an adult with trait c gives birth to a mutant juvenile with trait $c + \Delta c$ or $c - \Delta c$ with equal probability). Nonspatial simulations were realized using an individual-based stochastic model with global reproduction to a random empty site and global interactions of adults with a random juvenile. Alternatively, we can also simulate the nonspatial model by scrambling the whole lattice at each time step so as to obtain a well-mixed population (Wilson 1998). We have also used a square or a random lattice or a normal distribution of mutations. These different assumptions do not affect the qualitative results.

We present in figure 2 the evolutionary trajectories of the mean adult investment for different realizations of the spatial and nonspatial stochastic processes under the assumption of a linear trade-off between adult investment and reproduction (e.g., $\gamma(c) = \gamma c$). Despite the variability due to stochasticity, the trend is clear: cannibalistic behavior is favored in the well-mixed population, while spatial structure promotes the evolution of care. Thus, global interactions and global migration promote cannibalism, and as interactions and migration become more localized, there is a reversal in the selective pressures, leading to the evolution of care.

Spatial Invasion Fitness and the Unit of Selection

To derive some explicit conditions for the spread of a rare mutation, we find analytical models of spatial ecological dynamics to be useful because they can be embedded in more general frameworks such as population genetics (Rousset 2004) or adaptive dynamics (Metz et al. 1992; Geritz et al. 1998) in order to link ecology and evolution. Here, we use the correlation equations approach (Matsuda et al. 1992; Rand 1999); that is, we track the dynamics of spatial moments. Several previous studies (van Baalen and Rand 1998; Boots and Sasaki 1999; Le Galliard et al. 2003, 2005; Lion et al. 2006) have shown that correlation equations can be used to derive an explicit analytical expression for the invasion fitness of a rare mutant in a spatially structured resident population. The distinct feature of our approach is that we show that we can get some insight into the selective pressures on the trait without knowing the full dynamics of the system.

We focus on the dynamics of the expected densities of juveniles (p_J) and adults (p_A) in the resident population, which are given by the following equations (app. A):

$$\begin{cases} dp_J/dt = b_A q_{o/A} p_A - (\delta_J + \mu) p_J \\ dp_A/dt = \mu p_J - d_A p_A \end{cases}, \tag{3}$$

where $q_{o/A}$ is the local density of empty sites around an adult and δ_J and b_A are given by equations (1) and (2), respectively. The resident population reaches an equilibrium on the ecological timescale, and throughout the article, we denote the resident equilibrium densities with an asterisk (e.g., p_J^*, p_A^*, $q_{o/A}^*$). Three points are worth mentioning. First, these equations give the exact dynamics of the changes in expected densities of juveniles and adults, and no approximation of higher-order spatial moments is needed. Second, the full system of equations, giving the dynamics of the higher-order spatial moments, is not necessary to derive these equations, as shown in appendix A. Third, the effect of local or long-

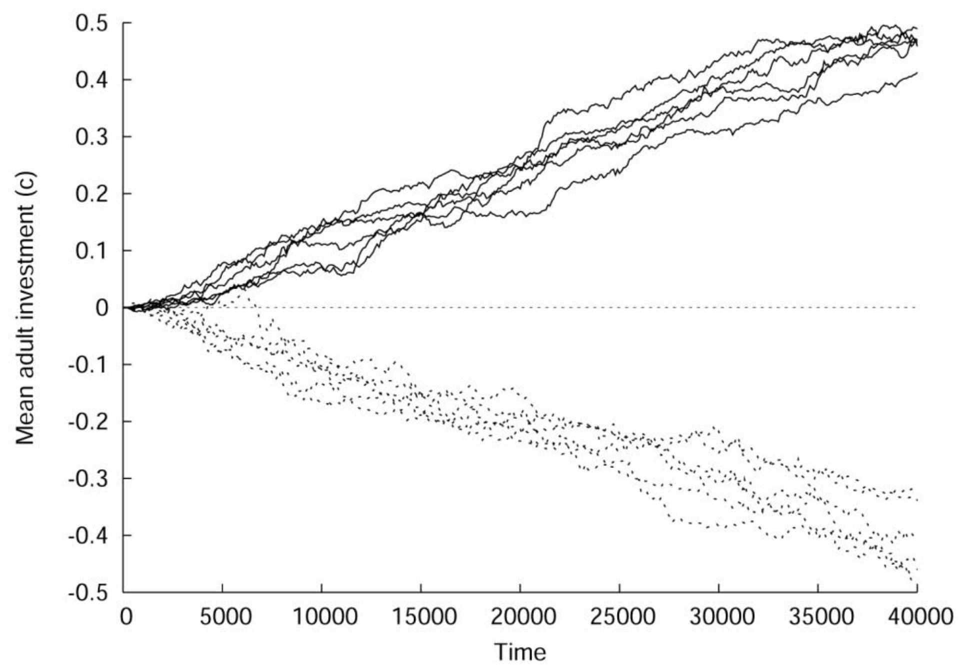

Figure 2: Evolution of adult behavior in spatial (*triangular lattice*, *solid*) and nonspatial (*dotted*) models. Six stochastic realizations are shown in each case, starting from $c = 0$. Parameter values: $b_0 = 4$, $d_J = 1.5$, $d_A = 1$, $\mu = 2$, $\gamma(c) = 0.4c$. Mutation rate: 0.004. Mutation step: $\Delta c = 0.01$. The time unit is the average duration of the reproductive (adult) stage. Lattice size: 100 × 100.

distance dispersal of juveniles (after birth) and adults is also included in those equations, but because dispersal events do not change the number of individuals, dispersal parameters do not appear in equation (3). How dispersal enters the problem is discussed later.

If we introduce a rare mutant (J', A'), the dynamics for the densities $p_{J'}$ and $p_{A'}$ are obtained from equation (3) by replacing J and A with J' and A'. If the mutant is rare, we can assume that the resident does not "feel" the presence of the mutant. However, because in a spatial model mutants will be clustered, mutant individuals will feel the presence of both resident and mutant individuals. This leads to the following average death and birth rates for the mutant:

$$\delta_{J'} = d_J - \beta c q_{A/J'} - \beta c' q_{A'/J'}, \tag{4}$$

$$b_{A'} = b_0 - \gamma(c')\frac{n-1}{n}(q_{J/A'o} + q_{J'/A'o}). \tag{5}$$

Note that although these rates depend on both the resident and the mutant traits, either directly or indirectly through the local densities, we refrain from stating this explicitly for notational simplicity.

When a mutant appears in a spatially structured population, it tends to form a cluster of mutant individuals (fig. 3) whose local structure is determined by the demographic parameters of both resident and mutant individuals. Whether this invading cluster expands or decays thus determines the fate of the mutant. Consequently, the per capita growth rate of a mutant depends on the local structure of the cluster. As shown by van Baalen and Rand (1998) and Ferrière and Le Galliard (2001), the invading cluster defines the relevant scale on which to define invasion fitness in spatially structured populations. A positive invasion fitness entails that the mutant will grow exponentially with a characteristic cluster structure (much like a stable age distribution in nonspatially structured populations). As van Baalen and Rand (1998) have pointed out, spatial invasion fitness and cluster structure must be computed at the same time so that the invading cluster represents a physical structure associated with fitness and can be interpreted as the relevant "unit of selection."

The novel aspect of this model is the fact that the mutant population is structured in age classes. Thus, to describe the fate of an invading mutant, we need to follow the densities of both juvenile and adult mutants. It turns out that the per capita growth rates of both classes are equal to the invasion fitness in the initial phase of invasion (app. B; for a more detailed treatment, see S. Lion and M. van Baalen, unpublished manuscript).

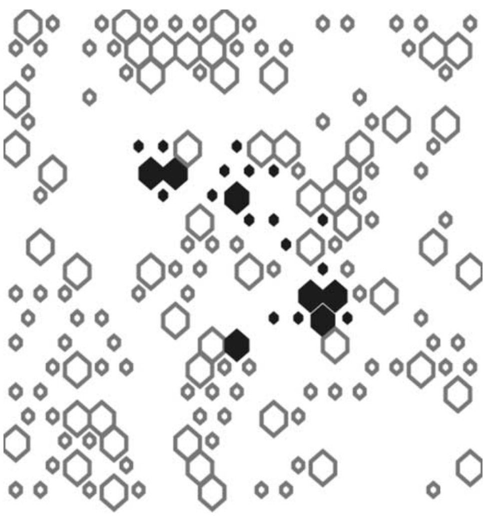

Figure 3: Typical snapshot of a cluster of mutants (*filled*) invading a resident population (*open*) on a triangular lattice. *Small hexagons* = juveniles. *Large hexagons* = adults.

The unit of selection is characterized by a precise local structure. Interestingly, it also has a precise stage structure that is directly determined by the spatial structure of the cluster. Indeed, we show in appendix B that the proportion of mutant juveniles in the cluster of mutants is given by

$$w_{J'} = \frac{p_{J'}}{p_{J'} + p_{A'}} = \frac{q_{J'/A'}}{q_{A'/J'} + q_{J'/A'}}. \qquad (6)$$

The important point is that when a mutant appears in the population, it will create and thus experience a different local structure but also, as a consequence, a different stage structure (e.g., the relative proportion of mutant juveniles may be greater or smaller than observed in the resident population).

Selective Pressures on Adult Behavior

We can use the definition of invasion fitness we just presented to derive the selection gradient for c, which gives information about the direction and potential endpoints of evolution. To avoid unnecessary technical details, we choose to present and analyze the main result without producing its derivation (which is given in app. E).

Selection Gradient

The expression we obtain for the selection gradient contains three components,

$$\frac{\partial \lambda}{\partial c'} \propto \beta \bar{q}_{J'/A'} + \frac{\partial b_{A'} q_{o/A'}}{\partial c'} + \beta c \frac{d_A}{\mu} \frac{\partial}{\partial c'} (q_{A/J'} + q_{A'/J'}), \qquad (7)$$

with everything being evaluated at $c' = c$ (meaning that we look at the selective pressures for a mutant close to the resident). A bar indicates that the local density is evaluated for a neutral rare mutant, that is, a mutant identical to the resident; the other local densities are associated with the unit of selection.

It is important to note that equation (7) is derived using solely an assumption of small mutations. In particular, we do not use any approximation of the spatial structure (e.g., moment closure approximations; Sato et al. 1994; van Baalen 2000). Equation (7) is therefore valid for any network structure, provided that the assumption of weak selection holds.

We can use equation (7) to recover the nonspatial selection gradient. In the mean-field model, the local density $\bar{q}_{J'/A'}$ becomes $p_{J'}$, which is 0 for a rare mutant. Likewise, the local densities $q_{A/J'}$ and $q_{A'/J'}$ converge to the global densities so that $q_{A/J'} + q_{A'/J'} = p_A + p_{A'} \approx p_A^*$, which does not depend on the trait of the mutant. Thus, the first and third terms of equation (7) vanish in the mean-field limit. Finally, the local density $q_{o/A'}$ is simply $p_o^* = 1 - p_J^* - p_A^*$, and the selection gradient for c in the nonspatial model reduces to

$$\frac{\partial \lambda}{\partial c'} \propto (1 - p_J^* - p_A^*) \frac{\partial b_{A'}}{\partial c'}. \qquad (8)$$

From equation (8), we see that if we assume a negative trade-off between adult investment and reproduction, the selection gradient will be negative in the nonspatial model, leading to the evolution of cannibalism, as shown in figure 2.

Selective Pressures

Equation (7) allows us to identify three components ("selective pressures") to the selection gradient, summarized in figure 4. The first selective pressure ($\beta \bar{q}_{J'/A'}$) is a measure of the efficacy of care, which depends on the clustering of mutant adults and mutant juveniles. Because $\bar{q}_{J'/A'}$ is always positive, the clustering of the mutants constitutes a positive pressure on the evolution of care. As spatial structure is destroyed (e.g., through an increase in migration rates), this pressure will become weaker because mutant adults and mutant juveniles will tend to be less aggregated. Ultimately, in the mean-field model, the selective pressure will vanish ($\bar{q}_{J'/A'} \approx p_{J'} = 0$), so that care will be counterselected. Thus, the term $\beta \bar{q}_{J'/A'}$ provides an explanation for the emergence of care in spatial models as opposed to nonspatial models. This also highlights how spatial structure can give rise to novel selective pressures. It must be kept in mind, however, that spatial structure is a two-edged sword and can also create selective pressures against care, as we shall see in the description of the second selective pressure. It is worth noting that assuming that the trait c affects nonlinearly the survival of juveniles (i.e., $\beta = \beta(c)$) would lead only to replacing $\beta \bar{q}_{J'/A'}$ with $(\partial\beta/\partial c')\bar{q}_{J'/A'}$.

The second selective pressure represents the marginal gain (or loss) in the reproductive output of adults resulting from a mutation in adult behavior. This pressure can be split into two components that represent the direct and indirect effect of adult behavior on adult reproduction,

$$\frac{\partial b_{A'} q_{o/A'}}{\partial c'} = q^*_{o/A} \frac{\partial b_{A'}}{\partial c'} + b_A \frac{\partial q_{o/A'}}{\partial c'}. \qquad (9)$$

The direct effect of adult behavior $(q^*_{o/A}(\partial b_{A'}/\partial c'))$ is also present in the nonspatial model (eq. [8]) and represents the cost of care due to the trade-off with reproduction. If caring for juveniles decreases the reproduction effort $b_{A'}$, the selective pressure will be negative. This component will be more important for low habitat saturation around adults ($q^*_{o/A}$ high). Here, we recover the classical expectation that a trade-off relationship sets an upper limit to the evolution of the trait. However, the costs due to the trade-off do not take the same form in the spatial and mean-field models. In the nonspatial model, we have (see app. A)

$$b_{A'} = b_0 - \gamma(c')(p_J + p'_J) \approx b_0 - \gamma(c')p^*_J,$$

which leads to the following expression of the trade-off:

$$\frac{\partial b_{A'}}{\partial c'} = -p^*_J \frac{\partial \gamma}{\partial c'},$$

whereas in the spatial model,

$$\frac{\partial b_{A'}}{\partial c'} = -\frac{n-1}{n} q^*_{J/Ao} \frac{\partial \gamma}{\partial c'} - \gamma(c)\frac{n-1}{n}\frac{\partial}{\partial c'}(q_{J/A'o} + q_{J'/A'o}).$$

An additional term $-\gamma(c)[(n-1)/n](\partial/\partial c')(q_{J/A'o} + q_{J'/A'o})$ appears that measures the marginal gain (or loss) in the local density of juveniles around a reproducing adult. In some cases, we may safely neglect this component. But the complete analysis helps us realize that this may not always be the case (although this component rightly vanishes when $\gamma(c) = 0$, e.g., at $c = 0$).

The indirect effect of adult behavior is $b_A(\partial q_{o/A'}/\partial c')$ and represents the marginal gain (or loss) of empty sites available for reproduction resulting from a mutation in adult behavior. It will be more important when the reproduction effort of adults b_A is high.

The third selective pressure $(\beta c(d_A/\mu)(\partial/\partial c')(q_{A/J'} + q_{A'/J'}))$ represents the marginal gain (or loss) due to the change in age structure of the invading cluster. It depends on the local density of adults around a mutant juvenile, the resident trait (βc), and the juvenile/adult ratio at ecological equilibrium ($d_A/\mu = p^*_J/p^*_A$). Because this pressure is proportional to the trait of the resident, it vanishes when the adults and the juveniles do not interact in the resident population ($c = 0$). Extensive numerical simulations (S. Lion and M. van Baalen, unpublished manuscript) confirm that this pressure is negligible.

When all selective pressures compensate, the selection gradient is 0, which indicates an evolutionary singularity. Adaptive dynamics methodology can then be used to investigate the evolutionary stability of this singularity. The precise form of the trade-off will then become very important in determining the number of evolutionary singularities and their stability (Kamo et al. 2006).

Interage Relatedness

An important ingredient of the selection gradient is the local density of adults as seen by juveniles, $\bar{q}_{J'/A'}$. Our model is a special case of a general class of models involving pairwise interactions between a donor and a recipient. In such models, invasion fitness depends on the relatedness of the recipient to the donor (Grafen 1982), and Day and Taylor (1998) have shown that the correct definition of relatedness for rare mutants is the probability that the recipient is a mutant, conditional to the fact that the donor is a mutant. This allows another interpretation of the local density $\bar{q}_{J'/A'}$. Because $\bar{q}_{J'/A'}$ gives the expected probability of finding a mutant juvenile in the neighborhood of a mutant adult, it is a measure of interage relatedness and is consistent with the expression of relatedness derived by

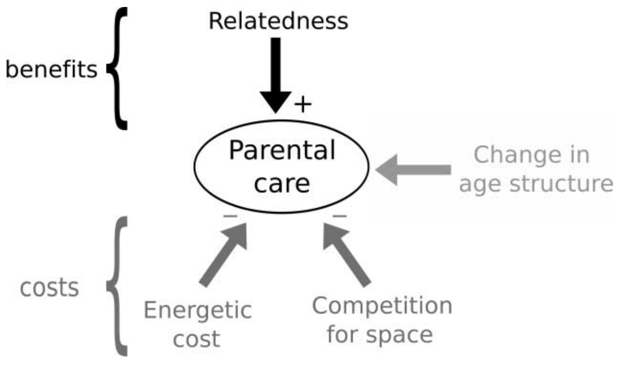

Figure 4: Summary of the selective pressures on parental care.

Day and Taylor (1998; see app. C for a more formal derivation).

An analytical expression for $\bar{q}_{J'/A'}$ can be obtained in the general case (S. Lion and M. van Baalen, unpublished manuscript), but it is rather messy and technical. To obtain a more interpretable expression of interage relatedness, we will make one exception to our rule of not using any moment closure approximation and work out the expression of $\bar{q}_{J'/A'}$ using standard pair approximation (Matsuda et al. 1992; see S. Lion and M. van Baalen, unpublished manuscript, for an explicit derivation). Moreover, we will only discuss the expression of $\bar{q}_{J'/A'}$ for c close to 0 and no migration (totally viscous population). Keep in mind, however, that standard pair approximation will yield a lower bound to the real value of relatedness because it tends to underestimate the clustering of mutants. The expression for interage relatedness is

$$\bar{q}_{J'/A'} = \frac{1}{n}\frac{b_0 q^*_{o/A}}{d_A + d_J + \mu}, \tag{10}$$

where n is the number of neighbors of a site and is a measure of population viscosity. If n is high, then each site is connected to many neighbors. In the limit $n \to \infty$, each site is connected to every other site, and we recover the mean-field limit. Therefore, as expected, $\bar{q}_{J'/A'}$ is 0 in the mean-field limit. With migration of juveniles or adults, an additional positive term appears on the denominator that is proportional to the rate of migration. Thus, increasing migration will disrupt the pattern of relatedness. This gives another way to recover the mean-field limit.

The numerator $b_0 q^*_{o/A}$ represents the reproductive output of a resident population at equilibrium. Using the fact that at equilibrium $q^*_{o/A} = (d_J + \mu)d_A/(b_A\mu)$ (see eq. [3]), we can further simplify this expression into

$$\bar{q}_{J'/A'} = \frac{1}{n}\frac{1/\mu}{[1/(d_J + \mu)] + (1/d_A)}, \tag{11}$$

which is population viscosity ($1/n$) times the average fraction of an adult's lifetime spent in the juvenile stage. Clearly, the selective pressure for care will be higher for high population viscosity (n small) and long duration of the juvenile stage. As the maturation rate increases, it will pay less to take care of juveniles.

When Should Adults Switch from Cannibalism to Parental Care?

In which direction will evolution take a population with no juvenile-adult interactions ($c = 0$)? If the spatial selection gradient is positive at $c = 0$, selection will favor positive values of c, leading to the evolution of care. If it is negative, care will be counterselected, and cannibalism results.

At the special point $c' = c = 0$, the selection gradient is simply

$$\frac{\partial\lambda}{\partial c'} \propto \beta\bar{q}_{J'/A'} + \frac{\partial b_{A'} q_{o/A'}}{\partial c'}. \tag{12}$$

Therefore, care will be selected over cannibalism if

$$\beta\bar{q}_{J'/A'} > -\frac{\partial}{\partial c'}(b_{A'} q_{o/A'})\Big|_{c'=0}. \tag{13}$$

The right-hand side of equation (13) is positive because care has a negative effect on adult reproductive output. Therefore, care evolves when the local density of related juveniles around an adult in the invading cluster is superior to the marginal loss in the expected reproductive output of an adult. Spatial clustering thus favors the evolution of blind altruism from adults to juveniles, which results in populations where adults tend to care more for related juveniles. Such indiscriminate parental care will not be favored when the fecundity cost of care outweighs the benefits. In this case, the population will evolve toward negative levels of investment, that is, infanticide or cannibalism. Because the local density of unrelated juveniles tends to increase when the local density of related juveniles decreases, another interpretation of the condition for the evolution of cannibalism is that it pays more to an adult to kill or eat neighboring juveniles when the probability that they are not related increases.

Both sides of equation (13) depend on the model parameters. The benefits of care ($\beta\bar{q}_{J'/A'}$) decrease when population viscosity increases and eventually vanish in a well-mixed population. Because competition for space is weaker in less viscous populations, the costs of care ($-\partial(b_{A'}q_{o/A'})/\partial c'$) also decrease when population viscosity decreases, but they eventually saturate, as shown by equation (8). Consequently, the benefits of care decrease faster than the costs when viscosity decreases, and there is a critical viscosity above which equation (13) does not hold any more and cannibalism is favored (fig. 5).

Inspection of the right-hand side of equation (13) shows that the marginal gain of cannibalism can be due either to a direct positive effect (an increase of mutant reproduction effort $b_{A'}$ through reallocation to reproduction of the energy extracted from consuming juveniles) or to an indirect positive effect (an increase of $q_{o/A'}$ corresponding to a reduction of competition for open space), a distinction emphasized by Claessen et al. (2004) in a recent review of the studies of cannibalistic populations.

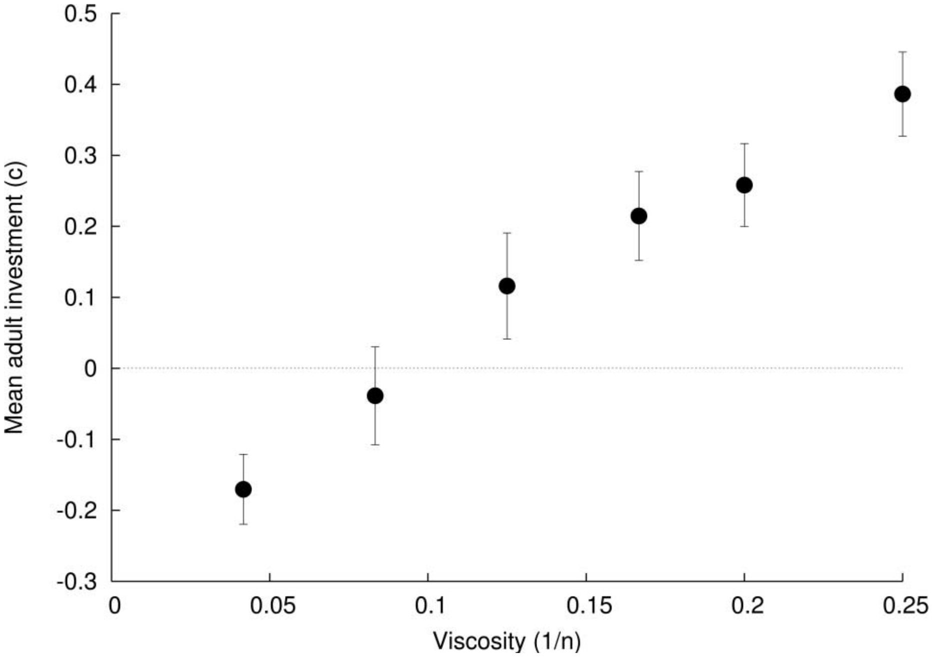

Figure 5: Mean adult investment after 30,000 generations in stochastic simulations on random networks of various connectivity. The average and standard deviation of 10 runs are shown. Note that the points do not represent evolutionarily stable investments. Mutation rate: 0.003. Other parameters as in figure 2.

Spatial Versions of Hamilton's Rule

Equation (13) amounts to a rediscovery of Hamilton's rule $Br > C$. Here, the benefits of parental care B are simply given by the conversion efficiency β, but the relatedness $r = q_{J'/A'}$ and the costs (right-hand side of eq. [13]) depend on local processes and spatial structure. Thus, relatedness and Hamilton's principle are recovered as emergent properties of the spatial system under consideration rather than postulated from first principles.

Our analysis is not restricted to the case where altruistic acts are directed to only one class. If we assume that adults interact in a similar fashion with other adults, with efficiency β_A (as opposed to $\beta = \beta_J$ for juveniles), equation (12) becomes (see app. E)

$$\frac{\partial \lambda}{\partial c'} \propto \beta_J \bar{q}_{J'/A'} + \frac{b_A q^*_{o/A}}{d_A} \beta_A \bar{q}_{A'/A'} + \frac{\partial b_{A'} q_{o/A'}}{\partial c'}. \tag{14}$$

A new term appears $((b_A q^*_{o/A}/d_A)\beta_A \bar{q}_{A'/A'})$ that represents the selective pressure on altruism due to helping other adults. We recognize a measure of relatedness ($\bar{q}_{A'/A'}$), weighed by the efficiency β_A and by a quantity that we can readily interpret as the product of adult fecundity ($b_A q^*_{o/A}$) times adult survival ($1/d_A$). In appendix D, we show that the reproductive value of adults in the resident population is equal to $b_A q^*_{o/A}/d_A$ when the reproductive value of juveniles is scaled to 1. Consequently, we can interpret equation (14) by noting that the benefits of an altruistic act directed to different age classes are weighted by the reproductive value of each class. This result is consistent with the conclusions of the kin selection models analyzed by Taylor (1990) and Taylor and Frank (1996), but here, it emerges as a natural property of the ecological model we consider. It is satisfying that different approaches lead to similar conclusions, and we advocate the notion that kin selection theory can be extended to include more complex ecological dynamics.

With a method similar to that used to derive equation (11), we can obtain an analytical expression for $\bar{q}_{A'/A'}$. For low investment of adults and no migration,

$$\bar{q}_{A'/A'} = \frac{1}{n} \frac{1/d_A}{[1/(d_J + \mu)] + (1/d_A)}, \tag{15}$$

which turns out to be quite similar to equation (11), but now population viscosity is weighted by the fraction of an adult's lifetime spent in the reproductive stage.

Link with Previous Unstructured Models

In the limit of high maturation rates ($\mu \to \infty$), the model collapses to the unstructured model with no juvenile class studied by van Baalen and Rand (1998) and Le Galliard et al. (2003). From equations (11) and (15), we see that, as should be expected, interage relatedness $\bar{q}_{J'/A'}$ vanishes, and $\bar{q}_{A'/A'}$ increases toward $1/n$ (an altruist has, on average, one altruist neighbor in the invading cluster), as found in the model of van Baalen and Rand (1998).

Also, the reproductive value of adults ($b_A q^*_{o/A}/d_A$) tends toward 1 for high maturation rates. If we use equation (14), the condition for the evolution of care becomes

$$\beta_A \bar{q}_{A'/A'} > -\frac{\partial b_{A'} q_{o/A'}}{\partial c'}, \qquad (16)$$

which is a spatial version of Hamilton's rule for unstructured populations (van Baalen and Rand 1998).

In our model, the benefits of altruism increase survival, and the costs decrease fecundity. In contrast, if we assume that the benefits and costs of altruism affect only fecundity (as in van Baalen and Rand 1998; Le Galliard et al. 2003), we will obtain a different expression where the marginal gain of altruism depends on the availability of empty sites (see app. F). This is because an individual can use a benefit only if she can effectively reproduce; that is, she must have an empty site in her neighborhood. Interestingly, if habitat saturation is low, there will be a high density of empty sites around an individual, so that selective pressure for open space $\partial q_{o/A'}/\partial c'$ becomes negligible, as shown by Le Galliard et al. (2005). Conversely, if the availability of empty sites decreases, the term of kin competition $\partial q_{o/A'}/\partial c'$ will become preponderant, which parallels the results of Taylor (1992*a*) and Wilson et al. (1992) that in an unelastic environment, the effects of kin selection and kin competition eventually cancel out each other (note, however, that those earlier models assumed nonoverlapping generations and no demographic stochasticity, which puts yet another barrier on the evolution of altruism; see, e.g., Taylor and Irwin 2000; Lehmann et al. 2006). Our analysis shows that in ecological models of kin selection, much attention must be given to how the costs and benefits of altruism affect an individual's life-history traits. The impact of kin competition will not be the same whenever altruism increases an individual's survival or her reproduction.

Discussion

This article provides three main results that we hope will help deepen our understanding of the evolutionary consequences of spatial ecological dynamics. First, we show that correlation equations can be used to derive analytical results on the evolution of care and cannibalism in a general model of juvenile-adult interactions. Second, we show that the selective pressures on parental care can be cast into the form of a variant of Hamilton's rule that is recovered as an emergent property of the ecological dynamics of the model. Third, we present a way to define invasion fitness in stage-structured, viscous populations. By doing so, we also shed some light on the level at which selection takes place in such populations. We first discuss in turn these three points, and then we address the more methodological aspect of our treatment and discuss a different approach to moment equations. We conclude by discussing some of the main limitations and perspectives of this study.

Selective Pressures on Parental Care and Cannibalism

We show that the evolution of adult investment in our model is determined by the balance between interage relatedness and the costs-to-benefits ratio. In other words, helping juvenile neighbors is favored when the benefits weighed by the average relatedness outweigh the reproductive cost of helping, which is the basic argument of Hamilton's rule. This cost incorporates both direct and indirect effects of helping: the energetic cost of helping can decrease the reproductive effort of the adult, but there is also an additional ecological cost due to the fact that decreasing juvenile mortality will increase competition for resources (here, by depleting the number of empty sites around an adult). This conclusion generalizes the result of van Baalen and Rand (1998) on the evolution of altruism to the case where altruistic interactions take place between individuals belonging to different classes. We also argue that our analysis supports the view that kin and group selection are two sides of the same coin in viscous populations (Grafen 1984; Queller 1994).

In this model, when relatedness is below the threshold for the evolution of parental care, cannibalism is favored if eating juvenile neighbors effectively increases the reproductive output of adults, either because of direct effects (allocation to reproduction of energy gained though cannibalism) or because of indirect effects (killing juveniles reduces the competition for space). Such trade-off between parental care and cannibalism is consistent with some empirical studies (Neff 2003; Manica 2004). It is also an example of "William's principle" (Sargent and Gross 1993), according to which cuckolded parents should switch to alternative investments. In our model, adults that run a high risk of helping nonrelated juveniles do best by cannibalizing juveniles. On the other hand, in the nonspatial version of our model, cannibalism is always favored because it increases adult fecundity through direct energetic effect. This actually represents an extreme case of the models of Stenseth (1985) and Skurdal et al. (1985), which predict that even if the gain of cannibalism is small, cannibalism by adults on juveniles can evolve if the young stages have low reproductive potential compared to the older stages, particularly in density-regulated populations, and if the reproductive output is concentrated in the last part of reproductive age. More generally, our analysis confirms the general verbal predictions of Polis (1988) that cannibalism and intraguild predation can readily evolve regardless of population structure in space because they provide the actor with a direct energetic benefit and an indirect benefit of decreased competition. On the other hand, evolution of altruistic (or spiteful) nonpredatory interference can evolve only via kin or group selection.

Our analysis shows that parental care can evolve even in the absence of kin discrimination. By helping juveniles in their neighborhood, adults are likely to help related juveniles. A combination of limited dispersal and "blind" altruism from adults to juvenile neighbors can thus be a stepping stone toward the evolution of parental care before active mechanisms of kin discrimination emerge. In the absence of such mechanisms, "helping all my young neighbors" is the more parsimonious rule that provides adults with inclusive fitness benefits (Hamilton 1964; Brown 1987; Mateo 2004). This is commonly observed in bird species with communal breeding, in which kin recognition is often absent and both the behavioral rule used by parents and relatedness are probabilistic, not certain (Brown 1987).

On a more theoretical note, our model reemphasizes the point made by Maynard Smith (1976, p. 282) that "it is not a necessary feature of kin selection that an animal should distinguish different degrees of relationship among its neighbors and behave with greater altruism to the more closely related." However, mechanisms of kin recognition can evolve, and evolutionary pressures on kin discrimination are likely to depend on the reliability of indiscriminate rules of parental behavior. As viscosity decreases (through increased dispersal of juveniles and/or adults), we expect mechanisms of kin discrimination to be favored. More generally, levels of parental care are expected to be negatively correlated with dispersal (but see Le Galliard et al. 2005 for a contrasting view).

Hamilton's Rule in Spatially Structured Populations

It is important to note that the emergence of a spatial version of Hamilton's rule is a robust feature of the evolution of cooperation in spatial models. Our analysis extends previous works by van Baalen and Rand (1998) and Le Galliard et al. (2003) to class-structured populations. We want to stress that apart from the assumption of weak selection, no approximation is needed to derive Hamilton's rule. Although the picture can be blurred by the fact that costs and benefits depend on demographic parameters and spatial structure, the evolution of cooperation in spatial models is favored by the initial clustering of mutants. Thus, ultimately, the invasion condition can be reduced to the form

$$Bq_{M/M} > C,$$

where $q_{M/M}$ measures the clustering of mutants and is, as we have discussed, a measure of relatedness; B and C are possibly complex functions depending on both physiological and ecological parameters and variables. When altruistic acts can affect different classes of recipients, the benefits accrued by each class of recipients must be weighted by the class reproductive value, as shown by Taylor (1990) and Taylor and Frank (1996) in nonspatial models of kin selection. Generally speaking, spatial versions of Hamilton's rule are an expected aspect of the evolution of cooperation in viscous populations because when reproduction is local and migration is low, parents and offspring tend to be aggregated, causing relatedness and spatial clustering to be two closely linked notions.

We believe this point to be important, especially because it has recently been argued that Hamilton's rule cannot be used to describe the evolution of viscous populations because of the inherent nonlinear dynamics of spatial games (Wenseleers 2006). As we will see, this opposite conclusion stems from a definition of invasion fitness that neglects spatial structure.

That being said, spatial versions of Hamilton's condition have the same limitations as those derived in other kin selection models. In particular, they can give information about the direction of selection and the location of the evolutionary singularities, but they teach us little as such on the final outcome of evolution (Doebeli and Hauert 2006). Whether the attracting singularity is an evolutionarily stable strategy or a branching point, for instance, is predicted by the second derivative of invasion fitness, whereas Hamilton's rules are derived from an analysis of the selection gradient. Likewise, we can expect Hamilton's rules to describe the expected evolutionary trajectories but not a single realization of the underlying stochastic process.

Invasion Fitness in Stage-Structured Viscous Populations

A novel result of this article is the expression for invasion fitness in stage-structured viscous populations. This expression is exact in that it gives the expected rate of increase of a rare mutant. Thus, importantly, our conclusions do not depend on any approximation, apart from the assumption of small mutations. In particular, this means that the emergence of a spatial version of Hamilton's rule is not based on particular closure methods being used, as it has been sometimes claimed (e.g., Wenseleers 2006).

As argued by van Baalen and Rand (1998), the spread of a rare mutation in such a population is best understood as the growth of a cluster of mutant individuals. Ecological dynamics shape the local structure of this cluster, which ultimately determines whether the mutant can invade. If the mutant population is structured in discrete classes, the cluster will be characterized by a precise stage structure, and each stage will have the same per capita growth rate in the initial phase of invasion (i.e., when the mutant is still globally rare). We argue that the structure of this cluster allows us to identify the level (or scale) of selection, and thus we can consider the expanding cluster as the unit of selection. Invasion fitness cannot be defined without characterizing the structure of the unit of selection.

Failure to define the invasion condition at the scale of the cluster will often result in incorrect conclusions. For instance, Wenseleers (2006) analyzed a spatial game of cooperation by computing the fitness of a single mutant and explicitly assuming that there is no relatedness in the spatial population. Because of the wide disagreement between his analysis and his simulations, he concluded that Hamilton's rule cannot be used in spatial games. However, the assumptions made on fitness and relatedness are valid only in the nonspatial version of the game. That spatial games can lead to patterns of relatedness was recognized by Doebeli and Hauert (2005) and further developed by Ohtsuki et al. (2006) and Taylor et al. (2007), although their results are derived in the case of constant population size. However, some confusion still surrounds this problem. In a recent review, Nowak (2006) suggests that cooperation on networks evolves via "network reciprocity," a mechanism that he claims is distinct from kin selection. We do not agree, as our analysis results in standard kin selection expressions.

The definition of spatial invasion fitness we use relies on the relaxation principle, which is a general feature of spatial models (Matsuda et al. 1992; Dieckmann and Law 2000). Local densities tend to be fast variables, so that they equilibrate quickly when the global density of the mutant is still very low. Rousset (2006) gives a welcome formal proof of the relaxation principle in spatially structured populations with constant size. However, demographic stochasticity is still not incorporated any further. Future work should identify the domain where relaxation principles can be used to simplify the analysis of spatially structured populations.

A more profound question pertains to the measurement of invasion fitness in the field. We predict that parental care should evolve only if interage relatedness is above a threshold, which makes sense in the light of the general theory of kin selection, but computing the value of the threshold from stochastic simulations is not a straightforward task. In the field, in addition, we will typically have access to only a sample of the whole population, which creates further statistical pitfalls, especially if the population is structured spatially. While the method we present in this article provides predictions and interpretations that fit well with current theory, application to empirical data will require statistical developments that allow us to link observations at the population level to predictions based on an invasion criterion.

On the Use of Moment Equations

This study was partly motivated by the realization that technicality and apparent lack of generality are pervasive to the literature on spatial ecology. Articles using moment equations, especially, typically rely on high-dimensional models and heavy notations, which at best frightens the less theoretically minded readers and at worst may lead to misrepresentation of the main results of the article. The popularization of moment equations under the label "pair approximation" has played an important role in understating the potentiality of the method of moments in both an ecological and an evolutionary context. Another important factor is that early articles using so-called pair approximations focused on ecological dynamics and aimed at matching as closely as possible the dynamics of stochastic simulations using various moment closure approximations. However, especially for weak selection, the spatial scale necessary to describe the ecological dynamics of a system (e.g., pairs) need not coincide with the spatial scale at which selective pressures take place (e.g., triplets or larger-scale correlations). In such cases, using moment approximations can either lead to ever-going refinements without much biological insight or introduce some artifacts in the evolutionary dynamics of the model.

In this article, we choose to avoid the use of moment closure approximations and focus on the exact (i.e., unclosed) equations that can be derived for the global and local densities. We show that by using only an assumption of small mutations, we can derive insightful analytical results on the selective pressures on the trait. Thus, we can use correlation equations as an independent modeling technique, much as the classical mean-field approach, without swamping the ecological and evolutionary meaningful questions in technical considerations. This does not imply sweeping the interesting details (and the devil) under the carpet. In order to get quantitative results, we need to pick a moment closure that accurately predicts the eco-evolutionary dynamics in the stochastic simulations. In a companion article (S. Lion and M. van Baalen, unpublished manuscript), we discuss the difficulties of such an undertaking. These details are of interest to people working in the field of spatial ecology, but they are not always necessary for other ecologists. We hope that the picture will change as more theoretical ecologists become familiar with the moment equations technique, but in the meanwhile, we believe that some important aspects of the evolution of spatially structured populations have been made obscure by the question of the quantitative match between stochastic simulations and their deterministic approximations.

Perspectives

We used parental care in the broad sense of care from adults to juveniles. Much of the literature about parental care reserves this denomination to care from parents to their offspring (Clutton-Brock 1991), which implies that the parents must be able to discriminate their kin and particularly their own offspring. An interesting extension of this work would involve modeling the joint evolution of care (or cannibalism) and recognition tags, extending recent work on the joint evolution of altruism and kinship signals (Jansen and van Baalen 2006). Moreover, our model excludes the possibility that cannibalism can be directed preferentially toward kin, but examples of such behaviors are frequent (Pfennig 1997), which calls for more refined ecological scenarios. Finally, the interesting question of parent-offspring conflict is excluded from our analysis partly because of the assumption of clonal reproduction.

The main limit of this work is certainly that it models adult behavior as a continuum of cannibalism and parental care. In nature, we can expect complex behavioral rules whereby an individual can choose to raise or kill its offspring depending on its state, the state of its offspring, or the environment. In other words, adults will often present plastic rather than fixed behaviors throughout their lifetimes. Some level of phenotypic plasticity could be introduced in the model in order to get more realism. Also, natural populations usually contain cannibalistic and noncannibalistic morphs. Much theoretical and empirical work has already been done on the dynamics of polymorph populations (Claessen et al. 2004), but evolutionary investigations remain scant. Building evolutionary models that combine spatial structure and cannibalistic polyphenism could be a daunting task yet could give rise to fruitful predictions.

Finally, in this article, we restricted our attention to the direction of selection and left aside the investigation of the potential evolutionary endpoints. A natural extension to this work, addressed by S. Lion and M. van Baalen (unpublished manuscript), is assessing the stability of the evolutionary singularities. Numerical investigation of the equations is then required, and the problem becomes the importantance of choosing the "correct" moment closure approximation to describe the dynamics on both the ecological and evolutionary timescales. The goal of such an approach is to derive improved pair approximations that accurately describe the attractor of the resident population and the local structure of the invading cluster of mutants. This remains an open problem and a question of paramount importance for future research.

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APPENDIX A

Expected Dynamics of Global Densities

In order to derive the deterministic equations for the global densities of juveniles and adults, one does not need to write down the full dynamics of the system. This becomes clear if one starts the analysis from the master equation.

Let us first consider an individual located at site x. If she is a juvenile, her death rate is $\delta_J(x)$, which gives the following expected change in the global density of juveniles due to mortality:

$$-\langle \delta_J(x)/x = J\rangle \mathrm{P}(x = J),$$

where $\mathrm{P}(x = J) = p_J$ is the probability of finding a juvenile on the network. We denote $\langle f\rangle$ the across-network expectation of a function f and $\langle f/x = i\rangle$ the conditional expectation of f given that site x is in state i. Thus, $\langle \delta_J(x)/x = J\rangle$ is δ_J, the average death rate of a juvenile. In a resident population, $\delta_J(x) = d_J - \beta(c)n_A(x)/n$, where $n_i(x)$ is the number of i neighbors of x. Thus,

$$\langle \delta_J(x)/x = J\rangle = d_J - \beta(c)\left\langle \frac{n_A(x)}{n}\middle/ x = J\right\rangle .$$

The term between angles is the average proportion of adults surrounding a juvenile, that is, $q_{A/J}$, which yields equation (1).

More care must be taken when deriving the birth term. Only adults that have an empty site in their neighborhood have a nonzero probability $b_A(x)$ of giving birth to an offspring. Thus, the expected change in p_J due to reproduction is

$$\langle b_A(x)/x = A, x \sim o \rangle \mathrm{P}(x = A, x \sim o),$$

where $x \sim o$ indicates that x has an empty site in its neighborhood. The probability $\mathrm{P}(x = A, x \sim o)$ is $p_{Ao} = q_{o/A} p_A$, the probability of finding a pair of sites A-o on the network. The average reproduction rate is calculated by taking the expectation on all sites x that are occupied by an adult and connected to an empty site, that is, on all pairs A-o. In the resident population, we have

$$\langle b_A(x) \rangle_{Ao} = \left\langle b_0 - \gamma(c) \frac{n_J(x)}{n} \right\rangle_{Ao} = b_0 - \gamma(c) \left\langle \frac{n_J(x)}{n} \right\rangle_{Ao},$$

where $\langle . \rangle_{Ao}$ indicates that the expectation is taken on all sites x occupied by an adult and connected to an empty site. Because we must take into account the fact that at least one neighbor is empty, this gives the following average birth rate:

$$b_A = b_0 - \gamma(c) \frac{n-1}{n} q_{J/Ao}.$$

Note that this quantity depends on triplet frequencies, as $q_{J/Ao} = p_{JAo}/p_{Ao}$, where p_{JAo} is the density of J-A-o triplets.

Finally, because maturation events do not depend (in this model) on a juvenile's environment, the equations for the expected dynamics of the global densities are

$$\frac{dp_J}{dt} = b_A q_{o/A} p_A - (\delta_J + \mu) p_J,$$

$$\frac{dp_A}{dt} = \mu p_J - \delta_A p_A.$$

To obtain the nonspatial model, we let go $n \to \infty$ and we replace $q_{J/i}$ and $q_{J/ik}$ with p_J, $q_{A/i}$ with p_A, and $q_{o/A}$ with $p_o = 1 - p_J - p_A$. In particular, this gives the following average birth rate:

$$b_A = b_0 - \gamma(c) p_J.$$

APPENDIX B

Spatial Invasion Fitness in Stage-Structured Populations

Local density $q_{i/j}$ is the ratio of the global density of pairs of sites in states i and j and of the global density of sites in state j: $q_{i/j} = p_{ij}/p_j$. This yields

$$\frac{dq_{i/j}}{dt} = \frac{1}{p_j} \frac{dp_{ij}}{dt} - \frac{q_{i/j}}{p_j} \frac{dp_j}{dt}.$$

In the initial phase of invasion, the cluster of mutants quickly reaches a pseudoequilibrium local structure (Matsuda et al. 1992; van Baalen and Rand 1998). This means that the time derivatives of the local densities as seen by the mutant are 0. The pseudoequilibrium values of the local densities characterize the local structure of the unit of selection.

If we denote by λ_j the per capita growth rate of j, we find, after rearrangement of the previous equation, that in the initial phase of invasion,

$$\frac{1}{p_{ij}}\frac{dp_{ij}}{dt} = \lambda_j.$$

Therefore, we can obtain an equation for $\lambda_{J'}$ (resp. $\lambda_{A'}$) by replacing i with A' and j with J' (resp. i with J' and j with A'). But because $p_{J'A'} = p_{A'J'}$ (pairs can be counted in both directions), we can write equivalently

$$\frac{1}{p_{J'A'}}\frac{dp_{J'A'}}{dt} = \lambda_{J'} = \lambda_{A'}$$

from which we deduce

$$\lambda = \frac{1}{p_{J'}}\frac{dp_{J'}}{dt} = \frac{1}{p_{A'}}\frac{dp_{A'}}{dt},$$

where λ is the invasion fitness. This result can be easily generalized to n stage populations. Moreover, because $p_{J'A'} = p_{A'J'}$, we have

$$\frac{p_{J'}}{p_{A'}} = \frac{q_{J'/A'}}{q_{A'/J'}},$$

from which we deduce equation (6),

$$w_{J'} = \frac{p_{J'}}{p_{J'} + p_{A'}} = \frac{q_{J'/A'}}{q_{J'/A'} + q_{A'/J'}},$$

and a similar expression for the relative proportion of mutant adults.

APPENDIX C

Relatedness

Following the treatment of Day and Taylor (1998), we derive the expression of relatedness for a rare mutant M in a spatial population with local donor/recipient interactions and haploid genetics. Our starting point is the definition (Michod and Hamilton 1980)

$$r = \frac{\mathrm{Cov}(D, R)}{\mathrm{Var}(D)},$$

where D and R are the genotypes of the donor and the recipient, respectively. We have

$$\mathrm{Cov}(D, R) = \mathrm{E}(DR) - \mathrm{E}(D)\mathrm{E}(R),$$

where $\mathrm{E}(DR)$ is the expected number of donor-recipient interactions between mutants. Thus, $\mathrm{E}(DR)$ is p_{MM}, the expected density of M-M pairs across the network, because altruistic interactions are assumed to be local. Likewise, $\mathrm{E}(D)$ and $\mathrm{E}(R)$ are given by the expected density of mutant individuals, so $\mathrm{E}(D) = \mathrm{E}(R) = p_M$, which gives $\mathrm{Cov}(DR) = p_{MM} - p_M^2 = (q_{M/M} - p_M)p_M$.

The variance term is

$$\mathrm{Var}(D) = \mathrm{E}(D^2) - \mathrm{E}(D)^2 = \mathrm{E}(D) - \mathrm{E}(D)^2 = (1 - p_M)p_M,$$

which gives the following expression for relatedness:

$$r = \frac{q_{M/M} - p_M}{1 - p_M}.$$

In the limit where the mutant is rare ($p_M = 0$), we obtain $r = q_{M/M}$, which is consistent with Day and Taylor's (1998) conclusion that relatedness for a rare mutant is the conditional probability that the recipient is a mutant, given that the donor is a mutant.

A possible extension of our model would allow interactions between individuals to take place either globally (with probability θ) or locally (with probability $1 - \theta$; see, e.g., Boots and Sasaki 1999). Then $\mathrm{E}(DR) = (1 - \theta)p_{MM} + \theta p_M^2$, and for a rare mutant, $r = (1 - \theta)q_{M/M}$. As the proportion of global interactions increases ($\theta \rightarrow 1$), relatedness decreases and eventually vanishes.

APPENDIX D

Class Structure and Reproductive Values

We can write the dynamics of the global densities of juveniles and adults in the resident population as

$$\frac{d}{dt}\begin{pmatrix} p_J \\ p_A \end{pmatrix} = \begin{pmatrix} -(\delta_J + \mu) & b_A q_{o/A} \\ \mu & -\delta_A \end{pmatrix}\begin{pmatrix} p_J \\ p_A \end{pmatrix},$$

where $\delta_i = d_i - \beta_i c q_{i/A}$. We know that right and left eigenvectors of the matrix will be proportional to the class frequency vector $\mathbf{u}$ and the vector of reproductive values $\mathbf{v}$, respectively (Taylor 1990). Because we assume that the resident population is at equilibrium, we are interested in the eigenvectors associated with eigenvalue 0, so that simple algebra readily yields

$$\mathbf{u} = \begin{pmatrix} 1 \\ \mu/\delta_A \end{pmatrix},$$

$$\mathbf{v} = \begin{pmatrix} 1 & \dfrac{b_A q_{o/A}^*}{\delta_A} \end{pmatrix}.$$

Thus, if the reproductive value of juveniles is set to 1, the reproductive value of adults is equal to $b_A q_{o/A}^*/\delta_A$ in the resident population at equilibrium.

Returning to equation (14) (where the selection gradient is evaluated at $c = 0$), we see that the benefits accrued by juvenile and adult recipients are weighted by their respective reproductive values. A full evaluation of the selection gradient for nonzero values of the resident trait leads to the same result (see app. E).

APPENDIX E

Deriving the Selection Gradient in the Spatial Model

We derive the expression of the selection gradient in the general case where adults can help (or kill) both juveniles and adults. Our starting point is the invasion dynamics of a mutant with trait c':

$$\begin{cases} dp_{J'}/dt = b_{A'} q_{o/A'} p_{A'} - (\delta_{J'} + \mu) p_{J'} \\ dp_{A'}/dt = \mu p_{J'} - \delta_{A'} p_{A'} \end{cases}, \tag{E1}$$

where $\delta_i = d_i - \beta_i c q_{A/i} - \beta_i c' q_{A'/i}$ for $i = J'$ or A'.

We will use the fact that in the initial phase of invasion, we can equate those equations to $\lambda p_{J'}$ and $\lambda p_{A'}$, respectively (see app. A), where λ is the invasion fitness. Thus, we obtain the following equation for λ after combining the two equations:

$$\lambda = b_{A'} q_{o/A'} \frac{\mu'}{\delta_{A'} + \lambda} - (\delta_{J'} + \mu).$$

Now, because the resident fitness is 0, we have

$$0 = b_A q^*_{o/A} \frac{\mu}{\delta_A} - (\delta_J + \mu),$$

where $\delta_i = d_i - \beta_i c q^*_{A/i}$ and $i = J$ or A.

Subtracting the last two equations, we obtain

$$\lambda = b_{A'} q_{o/A'} \frac{\mu}{\delta_{A'} + \lambda} - b_A q^*_{o/A} \frac{\mu}{\delta_A} - (\delta_{J'} - \delta_J). \tag{E2}$$

Now we make the assumption that the mutant is close to the resident ($c' = c + \partial c$), so that $\lambda = \partial\lambda$ is close to 0. We first look at the term $\delta_{J'} - \delta_J$:

$$\delta_{J'} - \delta_J = (d_J - \beta_J c q_{A/J'} - \beta_J c' q_{A'/J'}) - (d_J - \beta_J c q^*_{A/J}) = \beta_J (c q^*_{A/J} - c q_{A/J'} - c' q_{A'/J'}).$$

Invasion statistics $q_{A/J'}$ and $q_{A'/J'}$ can be Taylor expanded as follows:

$$q_{A/J'} = \bar{q}_{A/J'} + \partial q_{A/J'},$$
$$q_{A'/J'} = \bar{q}_{A'/J'} + \partial q_{A'/J'},$$

where the bar symbol denotes the local densities of a mutant that is identical to the resident. Such a mutant will see the same local density of adults as the resident, so that

$$\bar{q}_{A/J'} + \bar{q}_{A'/J'} = q^*_{A/J}. \tag{E3}$$

Then, we have

$$\delta_{J'} - \delta_J = \beta_J [c q^*_{A/J} - c(\bar{q}_{A/J'} + \partial q_{A/J'}) - (c + \partial c)(\bar{q}_{A'/J'} + \partial q_{A'/J'})].$$

If we use equation (E3) and neglect second-order terms, some terms cancel out, and we are left with

$$\delta_{J'} - \delta_J = -\beta_J [\partial c q_{A'/J'} + c(\partial q_{A/J'} + \partial q_{A'/J'})]. \tag{E4}$$

Now we want to Taylor expand the remainder of equation (E2). First, we note that

$$\begin{aligned}
\delta_{A'} &= d_A - \beta_A c q_{A/A'} - \beta_A c' q_{A'/A'} \\
&= d_A - \beta_A c(q_{A/A'} + \partial q_{A/A'}) - \beta_A (c + \partial c)(q_{A'/A'} + \partial q_{A'/A'}) \\
&= d_A - \beta_A c(q_{A/A'} + q_{A'/A'}) - \beta_A \partial c q_{A'/A'} - \beta_A c(\partial q_{A/A'} + \partial q_{A'/A'}) \\
&= d_A - \beta_A c q^*_{A/A} - \beta_A \partial c q_{A'/A'} - \beta_A c(\partial q_{A/A'} + \partial q_{A'/A'}) \\
&= \delta_A - \beta_A \partial c q_{A'/A'} - \beta_A c(\partial q_{A/A'} + \partial q_{A'/A'}).
\end{aligned}$$

Thus, we have

$$\frac{\mu}{\delta_{A'} + \lambda} = \frac{\mu}{\delta_A - \beta_A \partial c q_{A'/A'} - \beta_A c(\partial q_{A/A'} + \partial q_{A'/A'}) + \partial\lambda} = \frac{\mu}{\delta_A}\left[1 - \frac{\partial\lambda - \beta_A \partial c q_{A'/A'} - \beta_A c(\partial q_{A/A'} + \partial q_{A'/A'})}{\delta_A}\right],$$

and we can use this result to find

$$\begin{aligned} b_{A'} q_{o/A'} \frac{\mu}{\delta_{A'} + \lambda} &= (b_A + \partial b_{A'})(q^*_{o/A} + \partial q_{o/A'}) \frac{\mu}{\delta_A}\left[1 - \frac{\partial\lambda - \beta_A \partial c q_{A'/A'} - \beta_A c(\partial q_{A/A'} + \partial q_{A'/A'})}{\delta_A}\right] \\ &= b_A q^*_{o/A} \frac{\mu}{\delta_A} + \frac{\mu}{\delta_A}(q^*_{o/A} \partial b_{A'} + b_A \partial q_{o/A'}) - \frac{\mu}{\delta_A} \frac{b_A q^*_{o/A}}{\delta_A} [\partial\lambda - \beta_A \partial c \bar{q}_{A'/A'} - \beta_A c(\partial q_{A/A'} + \partial q_{A'/A'})]. \end{aligned}$$

We can plug this result and equation (E4) into equation (E2), and we find, after some rearrangements and taking the limit $dc \rightarrow 0$,

$$\left(1 + b_A \frac{\mu}{\delta_A^2} q^*_{o/A}\right) \frac{\partial\lambda}{\partial c'} = \beta_J \bar{q}_{A'/J'} + \beta_J c\left(\frac{\partial q_{A/J'}}{\partial c'} + \frac{\partial q_{A'/J'}}{\partial c'}\right) + \frac{\mu}{\delta_A} \frac{b_A q^*_{o/A}}{\delta_A}\left[\beta_A \bar{q}_{A'/A'} + \beta_A c\left(\frac{\partial q_{A/A'}}{\partial c'} + \frac{\partial q_{A'/A'}}{\partial c'}\right)\right] + \frac{\mu}{\delta_A} \frac{\partial b_{A'} q_{o/A'}}{\partial c'}.$$

At the special point $c = 0$, we have $\delta_A = d_A$, and the expression for the selection gradient collapses to

$$\left(\frac{d_A}{\mu} + \frac{b_A q^*_{o/A}}{d_A}\right) \frac{\partial\lambda}{\partial c'} = \beta_J \bar{q}_{J'/A'} + \frac{b_A q^*_{o/A}}{d_A} \beta_A \bar{q}_{A'/A'} + \frac{\partial b_{A'} q_{o/A'}}{\partial c'} \tag{E5}$$

if we use the fact that for a mutant identical to the resident, $\bar{q}_{A'/J'}/\bar{q}_{J'/A'} = \mu/\delta_A$. This gives equation (15).

APPENDIX F

Rederiving Hamilton's Rule in Le Galliard et al.'s (2003) Model

If maturation rates are very high, our model collapses to the model of Le Galliard et al. (2003) with only adult individuals. Then, the per capita growth rate of a rare mutant is

$$\lambda = b_{A'} q_{o/A'} - d_{A'}.$$

Le Galliard et al. (2003) assumed that the benefits and costs of altruism affect only an individual's fecundity, so that

$$\begin{aligned} b_{A'} &= b_0 + \beta_A c \bar{\phi} q_{A/A'o} + \beta_A c' \bar{\phi} q_{A'/A'o} - \gamma(c'), \\ d_{A'} &= d_A, \end{aligned}$$

where $\bar{\phi} = (n - 1)/n$. Note that the cost of altruism is assumed not to depend on an individual's environment, in contrast to our model.

This leads to the following expression for the selection gradient for c:

$$\frac{\partial\lambda}{\partial c'} = q^*_{o/A} \frac{\partial b_{A'}}{\partial c'} + b_A \frac{\partial q_{o/A'}}{\partial c'}.$$

For $c = 0$, this gives

$$\frac{\partial\lambda}{\partial c'} = q^*_{o/A}\left(\beta_A \bar{\phi} \bar{q}_{A'/A'o} - \frac{\partial\gamma}{\partial c'}\right) + b_0 \frac{\partial q_{o/A'}}{\partial c'},$$

so that the condition of invasion of an altruist mutant is

$$q^*_{o/A}\beta_A\bar{\phi}\bar{q}_{A'/A'o} > q^*_{o/A}\frac{\partial\gamma}{\partial c'} - b_0\frac{\partial q_{o/A'}}{\partial c'},$$

which is not quite Hamilton's rule yet because relatedness $\bar{q}_{A'/A'}$ does not appear in the equation. We need to take one further step.

First, recall that local densities $q_{i/jk}$ are given by p_{ijk}/p_{jk}, where p_{ijk} is the density of triplets *i*-*j*-*k* and p_{jk} is the density of pairs *j*-*k*. Second, it is equivalent to count *i*-*j*-*k* triplets and *k*-*j*-*i* triplets, so that $p_{ijk} = p_{kji}$. Thus, we have

$$q_{A'/A'o} = \frac{p_{A'A'o}}{p_{A'o}} = \frac{p_{oA'A'}}{p_{A'o}} = \frac{q_{o/A'A'}p_{A'A'}}{p_{A'o}} = q_{o/A'A'}\frac{p_{A'A'}}{p_{A'o}} = q_{o/A'A'}\frac{q_{A'/A'}}{q_{o/A'}}.$$

For a neutral mutant, we thus have, because $\bar{q}_{o/A'} = q^*_{o/A}$,

$$q^*_{o/A}\bar{q}_{A'/A'o} = \bar{q}_{o/A'A'}\bar{q}_{A'/A'},$$

so that the condition for the spread of altruism becomes

$$(\beta_A\bar{\phi}\bar{q}_{o/A'A'})\bar{q}_{A'/A'} > q^*_{o/A}\frac{\partial\gamma}{\partial c'} - b_0\frac{\partial q_{o/A'}}{\partial c'}.$$

(This must be contrasted with the condition obtained when the benefits of altruism affect survival and not fecundity [our model], in which case the condition for the spread of altruism is

$$\beta_A\bar{q}_{A'/A'} > q^*_{o/A}\frac{\partial\gamma}{\partial c'} - b_0\frac{\partial q_{o/A'}}{\partial c'}.$$

Thus, the condition for the evolution of altruism will not be the same depending on how costs and benefits affect fecundity or survival.)

Under the standard pair approximation, $\bar{q}_{o/A'A'} \approx \bar{q}_{o/A'} = q^*_{o/A}$, altruism evolves in Le Galliard et al.'s (2003) model if

$$(\beta_A\bar{\phi}q^*_{o/A})\bar{q}_{A'/A'} > q^*_{o/A}\frac{\partial\gamma}{\partial c'} - b_0\frac{\partial q_{o/A'}}{\partial c'}.$$

Le Galliard et al. (2003) have shown numerically that the pressure for open space $b_0\partial q_{o/A'}/\partial c'$ is negligible in their model, so that they obtain the following Hamilton's rule:

$$\beta_A\bar{\phi}\bar{q}_{A'/A'} > \frac{\partial\gamma}{\partial c'}.$$

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