

Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility

Jean-François Le Galliard,^{1,*} Régis Ferrière,^{1,2,†} and Ulf Dieckmann^{3,‡}

1. Fonctionnement et Evolution des Systèmes Ecologiques, Centre National de la Recherche Scientifique Unité Mixte de Recherche 7625, Ecole Normale Supérieure, 75005 Paris, France;

2. Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721;

3. Adaptive Dynamics Network, International Institute for Applied Systems Analysis, Schlossplatz 1, A-2361 Laxenburg, Austria

Submitted April 21, 2004; Accepted October 20, 2004;
Electronically published December 22, 2004

Online enhancements: appendices.

ABSTRACT: Social behavior involves “staying and helping,” two individual attributes that vary considerably among organisms. Investigating the ultimate causes of such variation, this study integrates previously separate lines of research by analyzing the joint evolution of altruism and mobility. We unfold the network of selective pressures and derive how these depend on physiological costs, eco-evolutionary feedbacks, and a complex interaction between the evolving traits. Our analysis highlights habitat saturation, both around individuals (local aggregation) and around unoccupied space (local contention), as the key mediator of altruism and mobility evolution. Once altruism and mobility are allowed to evolve jointly, three general insights emerge. First, the cost of mobility affects the origin of altruism, determining whether and how quickly selfishness is overcome. Second, the cost of altruism determines which of two qualitatively different routes to sociality are taken: an evolutionary reduction of mobility, resulting in higher habitat saturation, is either preceded or followed by the adaptive rise of altruism. Third, contrary to conventional expectations, a positive correlation between evolutionarily stable levels of altruism and mobility can arise; this is expected when comparing populations that evolved under different constraints on mobility or that differ in other life-history traits.

Keywords: evolutionary dynamics, spatial invasion fitness, altruism, mobility, habitat saturation, kin selection.

Sociality is an essential characteristic of life. It involves specific individual behaviors that lead to the emergence of collective properties, new levels of natural selection, and the adaptive complexification of living systems (Michod 1999). One of the intriguing features of sociality is that it causes a double cost to individuals. Sociality typically requires, first, some form of altruistic behavior through which individuals sacrifice their own fitness for the benefit of others (Hamilton 1964*a*, 1964*b*) and, second, some reduction in individual mobility, allowing for sustained interaction, which exacerbates competition for local resources (Frank 1995; Perrin and Lehmann 2001). The benefits associated with these costs must be substantial enough that the involved genes are not eliminated by natural selection. Thus, one of the challenges facing evolutionary theory is to explain the role of adaptive evolution in molding individual altruism along with the underlying population structure to help us understand the wide diversity of social systems observed in the wild (Choe and Crespi 1997; Crespi 2001).

The double cost of sociality reflects only some of the selective pressures acting on social traits. Low individual mobility may increase genetic relatedness between interacting individuals, thus promoting inbreeding as well as the evolution of helping behaviors through kin selection (Hamilton 1964*b*). Yet, the enhancement of neighbors' performance through altruistic interaction may also induce habitat saturation and thus exacerbate local competition among kin (Grafen 1984; Queller 1992). Increased competition between relatives for local resources can in turn reduce or even totally negate the indirect genetic benefits of altruism (Taylor 1992; Wilson et al. 1992). The deleterious effects of kin competition resulting from low mobility have been demonstrated in a recent comparative study of social traits in fig wasps. In these insects, strict philopatry of males competing for mates results in extremely strong local competition, which nullifies any indirect genetic benefits of decreasing aggressiveness toward

* Present address: Centre for Ecological and Evolutionary Synthesis, University of Oslo, P.O. Box 1050, Blindern, Oslo NO-0316, Norway; e-mail: j.f.l.galliard@bio.uio.no.

† E-mail: ferriere@biologie.ens.fr.

‡ E-mail: dieckmann@iiasa.ac.at.

relatives (West et al. 2001). In other social insects, limited dispersal can lead to competition between colonies founded by relatives (Thorne 1997). In cooperatively breeding vertebrates, local recruitment can also cause competition among relatives for dominance and breeding opportunities within a group (Clutton-Brock 2002). In general, the balance between kin cooperation and kin competition affecting the evolution of altruism is bound to vary with the species' life-history profile, the spatial scale over which cooperation and competition occur, and the underlying habitat structure (Queller 1992; Kelly 1994).

In a recent study, Le Galliard et al. (2003) presented the analysis of a model accounting for population viscosity (limited dispersal of offspring at birth) combined with adult mobility, overlapping generations, and fluctuations in local population size caused by local interactions and demographic stochasticity. In that model, the costs of local competition do not completely negate the benefits of kin cooperation, a finding echoed by other recent theoretical analyses (Mitteldorf and Wilson 2000; Irwin and Taylor 2001). That study also highlighted the critical influence individual mobility exerts on the evolution of altruism: high altruism could evolve only in species with low mobility, whereas the evolutionary trajectory of highly mobile species was halted in a state of "quasi selfishness." However, the assumption (made in that and many other studies) of mobility being fixed is appropriate only if mobility is strongly constrained by the environment or the genetic system. Otherwise, mobility and altruism will be entangled in joint evolution: costs and benefits of altruism depend on local spatial structures and thus on mobility (Ferrière and Le Galliard 2001; Perrin and Lehmann 2001), while costs and benefits of mobility depend on the amount of help on offer as well as on habitat saturation, which are both affected by altruism (Emlen 1997; Helms Cahan et al. 2002). The purpose of this study is to develop a unifying approach to address this fundamental feedback in the evolution of sociality.

Extending the framework used by Le Galliard et al. (2003), we study the joint evolution of altruism and mobility in a model in which individuals move and interact locally on a network of suitable sites (Matsuda et al. 1992; van Baalen 2000). The notion of fitness that is appropriate for characterizing frequency-dependent selection as it occurs in such a model is invasion fitness, that is, the per capita growth rate of a mutant when rare in the environment set by the wild-type population (Metz et al. 1992). This notion has been found to extend to kin selection processes involving diallelic, haploid genetics (Frank 1998). Extending work by van Baalen and Rand (1998), we derive invasion fitness from a set of correlation equations describing the population's spatial structure (Ferrière

and Le Galliard 2001; Le Galliard et al. 2003). On this basis, we then deduce the selective pressures acting on altruism and mobility traits and relate these pressures to the model's underlying parameters, we analyze the trajectories of the joint evolution of these traits and their interplay with the population's spatial structure, and we make predictions about the correlation patterns between altruism and mobility induced by evolution in response to variation of life-history traits or to ecological constraints across species or populations.

Model Description

In this model, interactions and mobility are local processes occurring between neighboring sites of a social network. Altruism and mobility are quantitative characters affecting the demographic parameters of individuals. The resulting individual-based dynamics mold the local population structure from which the selective pressures on altruism and mobility arise. These pressures, in turn, determine the evolutionary outcomes we aim to understand. All parameters and variables are listed in table 1.

Population Dynamics on Social Networks

Individuals are distributed over a network of sites. Each site may be empty or occupied by one individual and is randomly connected to n other sites that define a neighborhood; n is a fixed parameter measuring the neighborhood size, or "habitat connectivity." Such spatial structure is used classically to study social interactions (e.g., Rand 1998) and is typical of, for example, some vertebrates that defend territories and move primarily among adjacent sites. We use a continuous-time model in which generations overlap. During any small time interval, an individual may move to an empty site within its neighborhood, produce an offspring that is placed in an empty neighboring site, or die. The population is "viscous" (Hamilton 1964a, 1964b) in the sense that offspring may be laid only in sites neighboring a parent's (not farther off), yet mobility is permitted at any age unconditionally to the occurrence of birth events. Thus, our notion of mobility differs from that of "natal dispersal" but is similar to "breeding dispersal," which refers to an adult moving between different breeding sites. The per capita mobility rate m and death rate d are unaffected by local interactions. Mobility is costly to individuals, with a negative effect on the individual's intrinsic birth rate (Cohen and Motro 1989). The cost of mobility linearly impacts the intrinsic birth rate such that the net per capita birth rate (in the absence of interaction) is given by $b - \nu m$, where b measures the intrinsic per capita birth rate of sessile organisms and ν measures the cost sensitivity to the mobility rate.

Table 1: Notations used in this article

Notation	Definition
Model parameters:	
n	Neighborhood size (habitat connectivity)
$\phi = 1/n$	Probability to draw a connection at random within a given neighborhood
b	Intrinsic per capita birth rate
d	Intrinsic per capita death rate
m	Intrinsic per capita mobility rate (adaptive trait)
u	Intrinsic per capita rate of investment in altruism, or altruism rate (adaptive trait)
$C(m, u)$	Cost of mobility and altruism diminishing the birth rate
κ	Cost sensitivity with respect to the altruism rate
γ	Cost acceleration with respect to the altruism rate
ν	Cost sensitivity with respect to the mobility rate
k	Mutation probability per birth event
σ^2	Mutational step variance
Model variables:	
$n_{k i}(z)$	Number of sites in state k neighboring a site in state i at location z
$n_{k ij}(z)$	Number of sites in state k neighboring a site in state i within a pair ij at location z
N_i	Number of sites in state i
N_{ij}	Number of pairs in state ij
$q_{i j}$	Average local frequency of sites in state i neighboring a site in state j
$q_{i jk}$	Average local frequency of sites in state i neighboring a site in state j within a pair jk

Note: Subscripts x and y refer to a resident and a mutant phenotype, respectively.

Two types of local density-dependent factors affect movement and reproduction. First, both events are conditional on the availability of a neighboring empty site: consequently, local crowding negatively affects the rates of mobility and birth. Second, reproduction is enhanced by altruistic interactions with neighbors, inducing a positive effect of local crowding. Thus, an altruistic donor improves the quality of the neighboring sites at the expense of its own reproduction, as has been documented in some cooperatively breeding vertebrates (Cockburn 1998). In our model, the altruism rate u is defined by the per capita rate of energetic investment into altruistic interactions. Altruistic behavior is directed evenly toward all neighboring sites, regardless of the presence or phenotypes of neighbors. Consequently, every neighbor of a focal individual that invests at rate u into altruism sees her birth rate augmented by the amount u/n . We use the terms “selfishness” and “quasi selfishness” to describe, respectively, phenotypes whose investment in altruism is 0 or nearly 0.

Typically, altruism carries a physiological cost. For example, adult suricates *Suricata suricatta* lose significant body weight during babysitting activities (Clutton-Brock et al. 1998). In general, such a cost can depend on the level of altruistic investment in an accelerating, linear, or decelerating way. With an accelerating cost, the marginal costs of altruism increase with the level of altruism. Conversely, decelerating costs imply that increasing altruism at low levels is more costly than at high levels. In the

limiting case of linear costs, marginal costs are independent of the level of altruism. These three patterns are captured by the expression κu^γ , where κ scales the cost sensitivity to the altruism rate and γ determines whether costs are accelerating ($\gamma > 1$), linear ($\gamma = 1$), or decelerating ($\gamma < 1$). The combined cost of mobility and altruism diminishing the birth rate is given by $C(m, u) = \nu m + \kappa u^\gamma$.

Evolutionary Dynamics on Social Networks

The two traits evolving in our model are the altruism rate u and the mobility rate m . Mutations, which occur with a fixed probability k per birth event, cause these rates to differ between offspring and parent. Increments or decrements resulting from mutations are drawn randomly from a normal probability distribution with zero mean and variance σ^2 (identical for both traits) and without genetic correlations. Like in Le Galliard et al. (2003), we used the minimal process method (Gillespie 1976) to simulate the evolutionary process on a social network of 900 sites, generated by randomizing the edges of a 30×30 regular lattice with von Neumann neighborhoods and periodic boundaries.

In a large population in which mutations are rare and mutational steps are small, the stochastic mutation-selection process described above can be approximated by a deterministic process whose trajectories are the solution

of the canonical equation of adaptive dynamics (Dieckmann and Law 1996) applied to this model,

$$\frac{d}{dt} \begin{pmatrix} m_x \\ u_x \end{pmatrix} = k \frac{\sigma^2}{2} N_x \begin{pmatrix} \frac{\partial s_x(y)}{\partial m_y} \\ \frac{\partial s_x(y)}{\partial u_y} \end{pmatrix}_{y=x}, \quad (1)$$

where $x = (m_x, u_x)$ denotes a resident phenotype and $y = (m_y, u_y)$ denotes a mutant phenotype; N_x is the resident population size at population dynamical equilibrium, and $s_x(y)$ denotes the invasion fitness of a mutant phenotype y in a resident population of phenotype x . The selection gradient (term in parentheses on right-hand side) is a vector determining the expected local direction of the adaptive process. Equation (1) extends the classical description of trait dynamics along fixed adaptive landscapes to models in which the eco-evolutionary feedback between individual traits and the selective environment is made explicit (Dieckmann and Law 1996; Abrams 2001).

The equilibria of equation (1) are the phenotypes for which both components of the selection gradient vanish and are called evolutionarily singular phenotypes (Metz et al. 1992). A full stability analysis of these singularities requires independently examining their evolutionary attractivity or convergence stability and their noninvasibility or evolutionary stability (Eshel 1983; Geritz et al. 1998). Local evolutionary attractivity of a singularity (m^*, u^*) means that trajectories starting in its vicinity converge to the singularity. This is guaranteed when the eigenvalues of the Jacobian matrix of equation (1) have negative real parts. The local noninvasibility of a singularity means that all mutants in its vicinity are unable to invade. This is guaranteed when the eigenvalues of the Hessian matrix of invasion fitness (containing the second derivatives with respect to the mutant phenotype) are negative (Marrow et al. 1996). Convergence and evolutionary stability can also be characterized globally, respectively, through plotting phase portraits of adaptive trajectories and through pairwise invasibility plots (showing the sign of invasion fitness $s_x(y)$ as a function of x and y ; Geritz et al. 1998).

Spatial Invasion Fitness

The invasion fitness of a mutant is defined as the per capita growth rate of its population when rare in the environment set by the resident population (Metz et al. 1992). In appendix A in the online edition of the *American Naturalist*, we present the construction of the population dynamics model for a single phenotype (x) inhabiting the network; then, we extend the model to describe the interaction between x and a mutant phenotype, y (see also Ferrière and

Le Galliard 2001; Le Galliard et al. 2003). Since all density dependence occurs between neighboring sites, the mutant's growth over the network depends on the expected frequencies $q_{x|y}$ and $q_{y|y}$ of sites occupied, respectively, by a resident (x) and a mutant (y) in the neighborhood of any focal mutant (Matsuda et al. 1992). Accordingly, the deterministic dynamics of mutant population size N_y are given by

$$\frac{dN_y}{dt} = \{[b + (1 - \phi)u_x q_{x|y} + (1 - \phi)u_y q_{y|y} - C(m_y, u_y)]q_{0|y} - d\}N_y, \quad (2)$$

where $\phi = 1/n$ is the probability to draw any one of the connections at random within a given neighborhood (see eq. [A2c] in app. A). The invasion fitness $s_x(y)$ is then given by the term in braces.

Equation (2) can be understood as follows. The per capita growth rate of mutants (braces) is obtained as the difference between their birth rate and their death rate d . To determine the former, the mutant's effective birth rate (brackets) is discounted by the frequency $q_{0|y}$ at which mutants find empty sites in their neighborhood. The effective birth rate is given by the intrinsic birth rate b , enhanced by the benefits of altruism and diminished by the mutant's cost $C(m_y, u_y)$ of mobility and altruism. The benefits of altruism derive from interactions between mutants and residents, $(1 - \phi)u_x q_{x|y}$, and between mutants and mutants, $(1 - \phi)u_y q_{y|y}$. In both cases, the altruism rates u_x and u_y of the mutant's neighbors are weighted by the frequencies $q_{x|y}$ and $q_{y|y}$ at which these neighbors occur in the mutant's neighborhood. The factor $1 - \phi$ accounts for the fact that empty and occupied sites surrounding the mutant cannot be chosen independently, since their numbers must sum to n .

Even though the invasion fitness in equation (2) depends only on probabilities of finding sites neighboring a mutant in certain states, the dynamics of these neighbors in turn depend on their neighbors. Therefore, a complete description of the mutant's population dynamics—and thus of the probabilities $q_{x|y}$, $q_{y|y}$, and $q_{0|y}$ in equation (2)—requires an infinite hierarchy of correlation equations, each one describing the spatial structure at a particular scale in relation to that at the next larger one (Dieckmann et al. 2000). Here, we use the method of pair approximation to close this exact system of equations at the scale of pairs (Matsuda et al. 1992; Morris 1997; see app. A). This method is accurate for random networks featuring randomly assigned connections between sites, as is assumed here. Regular habitat geometry, where interactions take place among the geographically closest sites, would compromise the use of the standard pair approx-

imation and require more refined approximations (Harada and Iwasa 1994; Ellner et al. 1998; van Baalen 2000). However, a limited set of selected individual-based simulations indicates that our qualitative findings obtained from a random network model extend to regular networks when using a regular square lattice (results not shown).

The initial population dynamics of a rare mutant involve two distinct phases (van Baalen 2000). First, a single mutant individual either dies without leaving any descendants or begins to invade locally until its neighborhood structure stabilizes at a pseudoequilibrium state characterized by $\tilde{q}_{x|y}$, $\tilde{q}_{y|y}$, and $\tilde{q}_{0|y}$. Conditional on nonextinction during this first phase, the mutant population expands or contracts while retaining its pseudoequilibrium correlation structure. Spatial invasion fitness is then calculated as the mutant population's growth rate during the second stage, thus ignoring the first stage dominated by drift (van Baalen and Rand 1998):

$$s_x(y) = [b + (1 - \phi)u_x\tilde{q}_{x|y} + (1 - \phi)u_y\tilde{q}_{0|y} - C(m_y, u_y)]\tilde{q}_{0|y} - d. \quad (3)$$

A positive fitness implies that the invasion process enters a third phase during which a mutant phenotype that is sufficiently similar to the resident generically displaces the resident (Geritz et al. 1998).

The pseudoequilibrium correlation structure of the mutant population is affected by the equilibrium correlation structure of the resident population, characterized by $\bar{q}_{x|x}$ and $\bar{q}_{x|0}$. The latter is obtained from a model of the monomorphic resident population (app. A), while the former can be derived from the dynamics of a dimorphic population, when the mutant phenotype is rare and the resident phenotype is at equilibrium (app. B in the online edition of the *American Naturalist*). The spatial statistics $\bar{q}_{x|x}$ and $\bar{q}_{x|0}$ refine the empirical notion of habitat saturation, as originally introduced by Brown (1978) and Emlen (1982). The probability $\bar{q}_{x|x}$ measures "local aggregation," that is, the level of crowding felt locally by any given individual. By contrast, the probability $\bar{q}_{x|0}$ measures "local contention," that is, the level of crowding around any vacant site, in which each neighbor might lay an offspring. Since the crowding around individuals can markedly differ from the crowding around empty sites, it is important to strictly distinguish between these two complementary dimensions of habitat saturation.

Selective Pressures on Mobility and Altruism

An analysis of the components of the selection gradient, as defined by equations (1) and (3), yields a full description of the selective pressures operating on altruism and mobility. This analysis is expounded in appendix B and reveals important general insights, which we describe next.

The first component of the selection gradient is the derivative of the spatial invasion fitness with respect to m and measures the total selective pressure on the mobility rate m :

$$\partial_m s_x(y) = \bar{q}_{0|x} \left\{ \left[\frac{d}{\bar{q}_{0|x}^2} - (1 - \phi)u_x \right] \partial_m \tilde{q}_{0|y} - \partial_m C \right\}, \quad (4)$$

where ∂_m denotes a derivative with respect to m_y , evaluated at $y = x$ (see eq. [B2] in app. B). The equation's right-hand side identifies the two competing components of this selective pressure: the marginal physiological cost of mobility, $\partial_m C$ (here $\partial_m C = \nu$), and the marginal gain (or loss) in open space resulting from altered mobility in the neighborhood of a mutant, $\partial_m \tilde{q}_{0|y}$, translated into a fitness change via a conversion coefficient (brackets) depending on death rate, habitat connectivity, altruism rate, and local aggregation $\bar{q}_{x|x} = 1 - \bar{q}_{0|x}$. This conversion coefficient decreases with decreasing local aggregation $\bar{q}_{x|x}$. Accordingly, the evolution of mobility is partially driven by the advantage conferred during invasion to mutants that are surrounded by more open space than residents. The marginal gain in open space $\partial_m \tilde{q}_{0|y}$ is a complex function of resident mobility and local contention; numerical analysis shows that it is little influenced by local aggregation (app. B).

The second component of the selection gradient is the derivative of spatial invasion fitness with respect to u , which measures the total selective pressure on the altruism rate u (see eq. [B3] in app. B). Extensive numerical simulations show that the marginal gain (or loss) in open space resulting from altered altruism in the neighborhood of a mutant can be neglected (see fig. 4 in Le Galliard et al. 2003), which yields

$$\partial_u s_x(y) = \bar{q}_{0|x} [(1 - \phi)\bar{q}_{y|y} - \partial_u C]. \quad (5)$$

The equation's right-hand side highlights the two competing components of this selective pressure: the marginal, physiological cost of altruism, $\partial_u C$, and the benefit of increased altruism among mutants, measured by $\bar{q}_{y|y}$, diminished by the discounting factor $1 - \phi$, which solely depends on habitat connectivity n . The term $\bar{q}_{y|y}$ measures the probability that the recipient of an action performed by a mutant individual is a mutant itself and thus provides a measure of relatedness (Day and Taylor 1998). Conse-

quently, equation (5) emphasizes the role of kin selection in the evolution of altruism. In appendix B, relatedness $\bar{q}_{y|y}$ is derived analytically:

$$\bar{q}_{y|y} = \frac{d\phi}{d + (1 - \phi)m\bar{q}_{0|x}}. \quad (6)$$

This expression shows that relatedness among mutants, and thus the marginal gain resulting from altruistic interactions between relatives, is higher in populations with an elevated local aggregation $\bar{q}_{x|x} = 1 - \bar{q}_{0|x}$ of the residents. Equation (6) also shows that the benefits of altruism rise with reduced mobility, lower habitat connectivity, or reduced mortality.

These results demonstrate that, besides the physiological costs associated with each trait, the evolutionary dynamics of altruism and mobility are mediated by two factors: eco-evolutionary feedback loops and selective interactions (fig. 1). Eco-evolutionary feedback loops result from the interplay between ecological variables and adaptive traits: in particular, such loops occur when the change in a trait value affects the population's spatial structure, which in turn modifies the selective pressures on that trait. Selective interactions in our model result from the interplay between altruism and mobility. Figure 1 offers a comprehensive overview of all eco-evolutionary feedbacks and selective interactions we have identified in the joint evolution of altruism and mobility. In this map, habitat saturation, specified in terms of both local aggregation and local contention, plays a central role.

Feedback between Habitat Saturation and Mobility

Habitat saturation is entangled with mobility through a negative feedback loop that operates along two separate pathways. First, according to our exhaustive numerical tests (app. B), increased mobility reduces the marginal gain of open space in equation (4). Second, increased mobility decreases local aggregation (through its costs on birth rate; app. A), which reduces the conversion coefficient in equation (4). Thus, effects along the two pathways identified here are acting synergistically to reduce the selective benefits of mobility as mobility increases in the population.

Feedback between Habitat Saturation and Altruism

Understanding this second feedback loop starts out from the fact that altruism generally increases local aggregation (through its positive effect on birth rate; app. A). Local aggregation, in turn, increases relatedness and, therefore, the benefits of kin cooperation described in equation (6), which favors the evolution of even more altruism according to equation (5). This results in a positive feedback

between local aggregation and altruism. In addition to the eco-evolutionary feedback, the evolution of altruism is also controlled by a physiological feedback (not represented in fig. 1) whenever the cost of altruism is nonlinear: for a decelerating (accelerating) cost, the marginal cost of altruism decreases (increases) with the level of altruism. This physiological feedback is thus positive for decelerating costs of altruism and negative for accelerating costs.

Selective Interactions between Altruism and Mobility

Figure 1 also allows deciphering the selective interactions between altruism and mobility, in which local aggregation is crucial. On the one hand, increasing mobility reduces relatedness according to equation (6) and therefore weakens the selective pressure in favor of altruism according to equation (5). On the other hand, increasing altruism strengthens local aggregation, which increases the conversion factor in equation (4) and therefore the selective pressure in favor of mobility: opening space by moving around is more beneficial when local aggregation is high. However, equation (4) shows that increasing altruism also has a direct, negative effect on this conversion coefficient: there is an increasing “benefit of philopatry” when neighbors are altruistic (Stacey and Ligon 1991). The net effect on the evolution of mobility thus depends on the balance between these two counteracting effects, which varies with the level of altruism: our numerical simulations reveal a net effect where the conversion coefficient is generically weakened for lowest rates of altruism and enhanced for intermediate and high altruism. Moreover, in species with accelerating costs, the physiological feedback described above implies that a rise of altruism severely diminishes fecundity, which results in reduced local aggregation, a diminished conversion coefficient, and hence a negative effect on the intensity of selection for opening space.

Separate Evolution of Altruism and Mobility

In general, the evolutionary dynamics of single traits are monotonous and converge to a point attractor (which, under certain circumstances, depends on the population ancestral state). Any small mutation arising around these singularities is selected against and fails to invade.

Altruism

The evolutionary dynamics of altruism primarily depend on the pattern of physiological cost of altruism (for more details, see Le Galliard et al. 2003). Under the assumption of decelerating costs, ancestral selfishness can be displaced only as a result of rare, large mutations. There is a “waiting time” for the adaptive rise of altruism that increases with

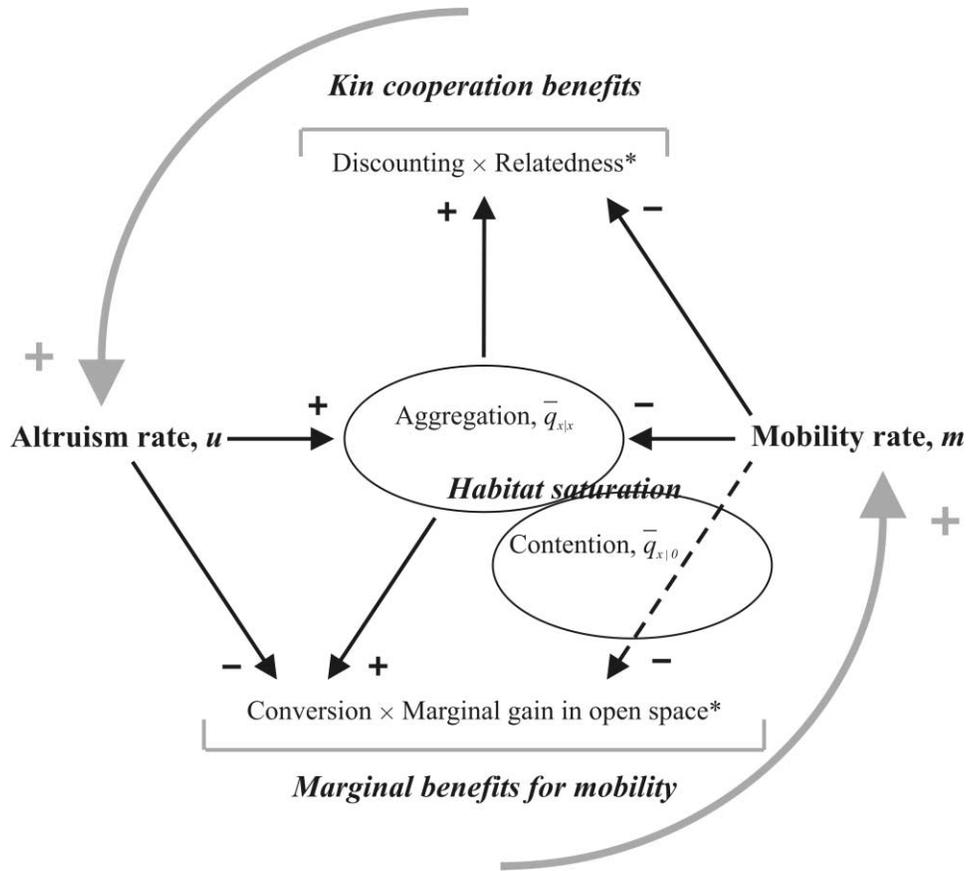


Figure 1: Selective pathways affecting altruism and mobility. All eco-evolutionary feedbacks and selective interactions can be traced on this diagram. Curved gray arrows indicate selective pressures. Plain arrows refer to positive or negative links established from the analysis of equations (4)–(6) (see also app. B in the online edition of the *American Naturalist*). The dotted arrow indicates a complex combination of direct and indirect (via local contention) effects of mobility on the marginal gain in open space. Asterisks indicate that relatedness and the marginal gain in open space are measured for a mutant during invasion.

the mobility rate. Only in the limiting case of a linear cost of altruism may pure selfishness remain unbeatable. This occurs in species with a “strong” linear cost, for which $\kappa > \phi(1 - \phi)$, and a mobility rate larger than the threshold (see eq. [8] in Le Galliard et al. 2003):

$$m_t = b \frac{\phi(1 - \phi) - \kappa}{\nu[\phi(1 - \phi) - \kappa] + \kappa(1 - \phi)}. \quad (7)$$

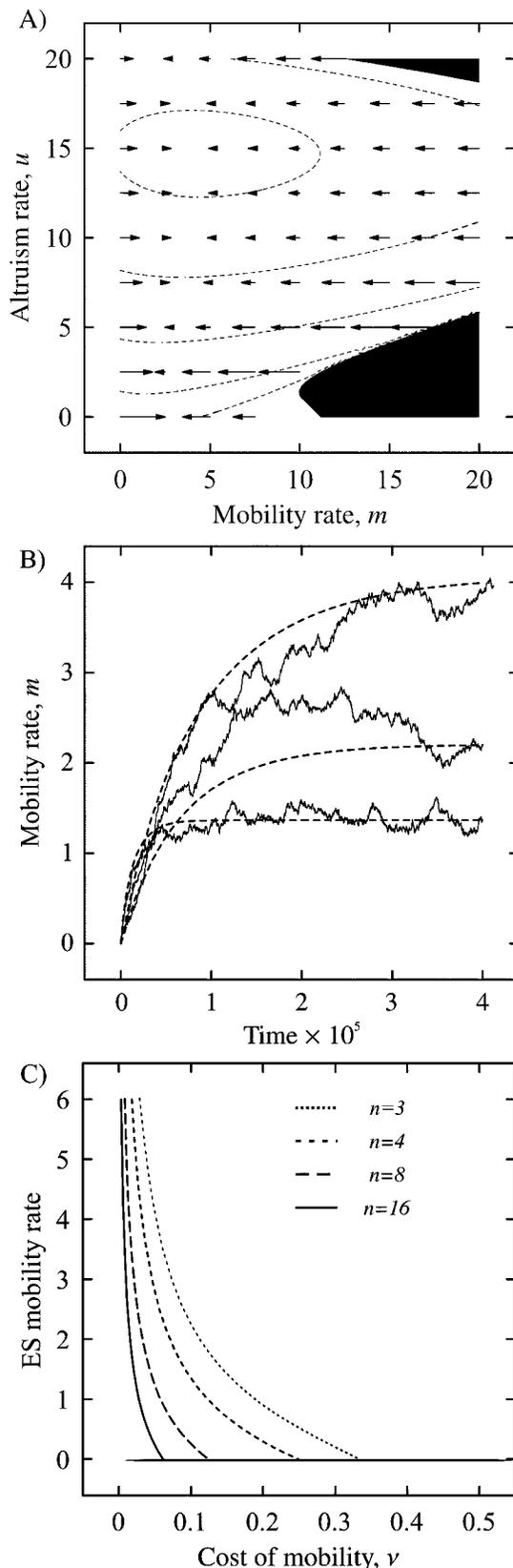
Thus, the evolution of altruism is hindered only when the most unfavorable conditions are enforced, combining a high cost sensitivity to altruism, high mobility, and high habitat connectivity.

In species with accelerating costs of altruism, the altruism rate evolving is lower in more mobile organisms. Under “rapidly” accelerating costs (high κ and/or γ much larger than 1), the relationship between mobility and selected altruism is smooth, and the selected rate of altruism

is always low. In contrast, under “slowly” accelerating costs (low κ and γ close to 1), the relationship between mobility and selected altruism shows a sharp discontinuity: high levels of altruism evolve in species with low mobility, whereas quasi selfishness evolves at high mobility. When mobility is low, the high level of altruism that evolves can be approximated as $u^* = [\phi(1 - \phi)/\kappa\gamma]^{1/(\gamma-1)}$ (see eq. [9] in Le Galliard et al. 2003), which depends only on habitat connectivity and the parameters affecting the physiological cost of altruism. At intermediate mobility, the evolutionary outcome depends on the ancestral state of the population: if the ancestral altruism is low, quasi selfishness evolves; otherwise, a high level of altruism is selected.

Mobility

Mobility as a single adaptive trait always evolves toward a globally attractive and uninvadable singularity (fig. 2A,



2B). In general, there is no analytical expression for the resulting evolutionarily stable (ES) mobility rate m^* , yet in the special case of a purely selfish species ($u = 0$), solving for the zeros of the first-order Taylor expansion of spatial invasion fitness with respect to m (see eq. [4]) yields

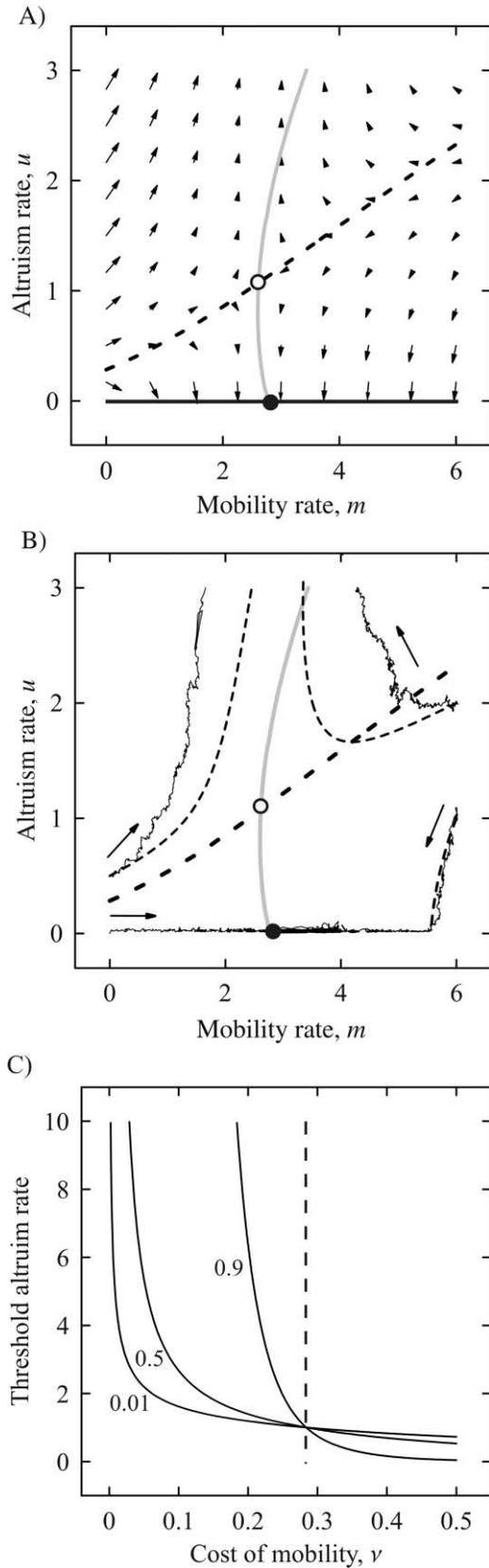
$$m^* = \frac{b[\sqrt{\nu(1-\nu)\phi(1-\phi)} - \nu(1-\nu)]}{\nu(1-\nu)[(1-\phi) - \nu]}. \quad (8)$$

Thus, in purely selfish species, the ES mobility rate decreases with an increasing cost of mobility ν and equals 0 when $\nu \geq \phi$ (fig. 2C); it also decreases with increasing habitat connectivity ($n = 1/\phi$; fig. 2C) and increases with the birth rate but is independent of the mortality rate. Furthermore, the value m^* given by equation (8) possesses the remarkable property of maximizing the local contention $\bar{q}_{x|0}$; thus, in purely selfish species, evolution of mobility alone maximizes habitat saturation around empty sites. Numerical simulations suggest that the same patterns persist at any level of altruism $u > 0$, except that higher mortality then results in a lower ES mobility rate.

The ES mobility rate m^* varies also with the species' degree of altruism u . The empirical expectation is that more altruistic species are less mobile, but the typical pattern is more complex. Zero mobility is selected for if the mobility cost is too high ($\nu > \phi$), irrespective of the degree of altruism. Otherwise, there may be a slight decrease of m^* as u increases through very small values, but m^* increases with u over a wide range of degrees of altruism (see fig. 3A for the case of a decelerating altruism cost, fig. 4 for a linear cost, and figs. 2A and 5 for accelerating costs). At very high values of u , m^* can decrease again with larger values of u in species with accelerating costs of altruism.

This pattern can be understood from the selective pressures that operate on m (see eq. [4]; fig. 1). Equation (4) shows that local aggregation and the altruism rate have opposite effects on the intensity of the selective pressure to open space. Furthermore, local aggregation itself depends on the altruism rate. At extremely low values of m ,

Figure 2: Evolutionary dynamics of mobility. *A*, Singular mobility rates for an accelerating cost of altruism. Gray curve, mobility isocline. Arrows, selection gradients. Dashed curves, contour lines of the local contention $\bar{q}_{x|0}$. Dark area, population extinction domain. Parameter values: $\gamma = 3$, $\kappa = 0.001$, and $\nu = 0.1$. *B*, Average of 10 independent stochastic simulations (continuous curves) and deterministic approximation (dashed curves) at $u_x = 0$ (two lower curves), $u_x = 20$ (two intermediate curves), or $u_x = 10$ (two upper curves). Mutation parameters: $k = 0.01$ and $\sigma = 0.01$. *C*, Evolutionarily stable mobility rates with respect to the cost of mobility for different values of habitat connectivity. Other parameter values as in *A*. Unless otherwise stated, $n = 4$, $b = 2$, and $d = 1$.



the dependency of local aggregation on u is weak. Therefore, as u increases, its direct, negative effect predominates, and m^* tends to decrease. Over a range of larger u , local aggregation rises rapidly with u , so that the indirect effect of u via local aggregation dominates: more mobility is selected for. A further increase of u causes a substantial reduction in birth rate for an accelerating cost of altruism and hence a decrease of local aggregation; this drives the evolution of less mobility.

Joint Evolution of Altruism and Mobility

Our analysis of the joint evolutionary dynamics of mobility and altruism develops from equation (1). The two corresponding isoclines generally cross at a single attractive and evolutionarily stable singularity (ESS), denoted by (m^*, u^*) . The main conclusions of our analysis are tested against numerical simulations of an individual-based model in which all approximations involved in the deterministic model (eq. [1]) are avoided.

Origin of Altruism

To investigate the origin of altruism, we assume a decelerating cost of altruism. Our previous analysis showed that in species characterized by such costs, the conditions under which altruism can evolve are the most stringent (Le Galliard et al. 2003). Also, in agreement with the classical empirical view, we assume that the selfish, ancestral state involves highly mobile individuals. Starting from selfishness associated with high mobility, mobility first decreases toward the critical value m^* given by equation (8) (see fig. 3A, 3B). The trait pair $(m^*, 0)$ is an endpoint of the deterministic dynamics in trait space. However, a different pattern applies when the stochasticity of the underlying individual-based process is taken into account. In a population where mutations may be large occasionally, mu-

Figure 3: Joint evolution of altruism and mobility with decelerating costs of altruism. *A*, Bistability in the evolutionary dynamics of altruism. For any mobility rate, the population evolves toward selfishness if initial altruism is below a threshold; above that threshold, higher altruism evolves. *Continuous gray curve*, attractive mobility isocline. *Continuous black curve*, attractive altruism isocline. *Dashed black curve*, repelling altruism isocline. *Arrows*, selection gradients. *Open circle*, repelling singularity. *Filled circle*, attractive singularity. Parameters values: $\gamma = 0.5$, $\kappa = 0.2$, and $\nu = 0.05$. *B*, Average of 10 stochastic simulations at four different initial conditions (*continuous curve*) and the deterministic predictions (*dashed curves*). Mutation parameters: $k = 0.01$, $\sigma = 0.01$. *C*, Threshold altruism rate for a mutant to invade a selfish resident at the ES mobility rate. Effect of the cost of mobility for different values of the cost acceleration. The limit case of a linear cost is indicated by a vertical dashed line.

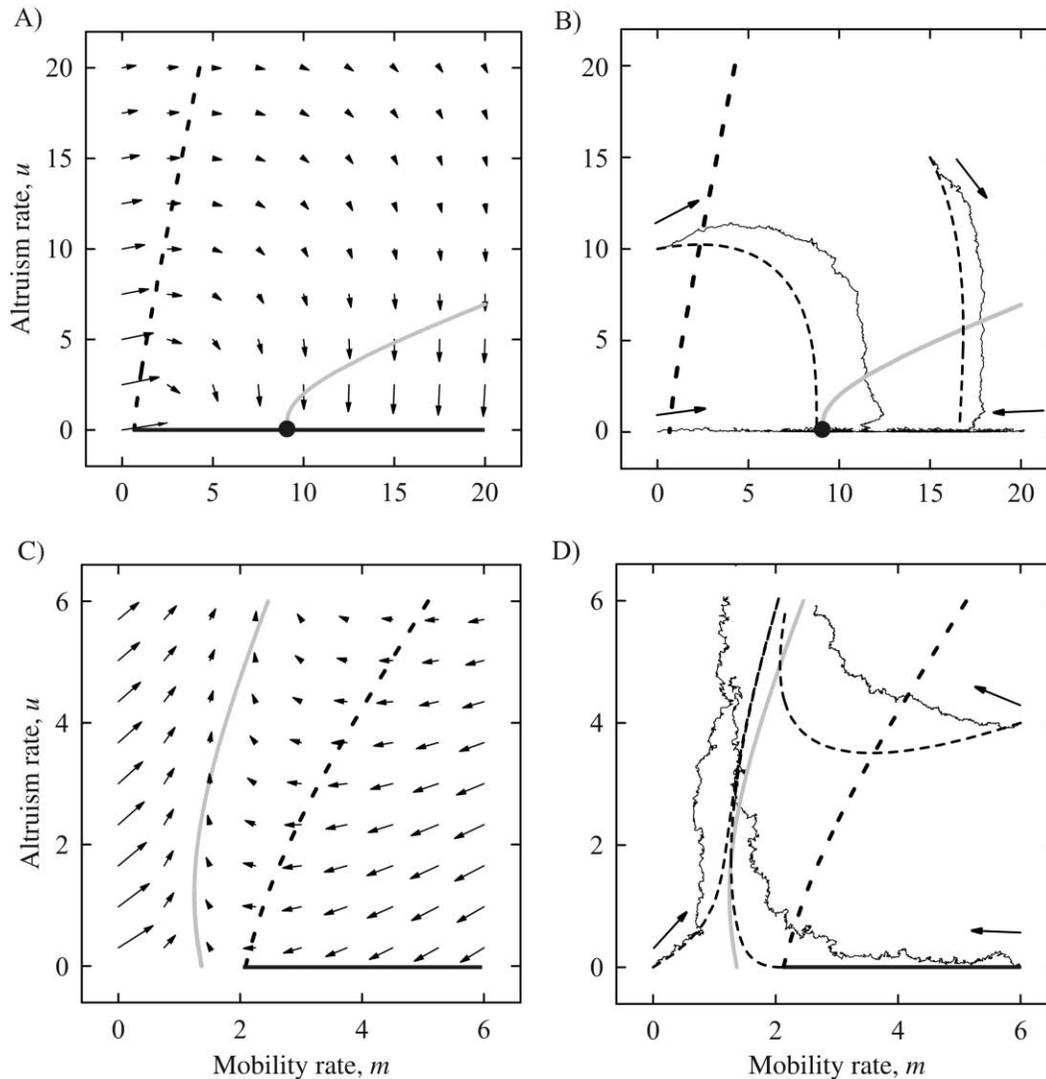


Figure 4: Joint evolution of altruism and mobility with a linear cost of altruism. *A*, Convergence to selfishness under low cost sensitivity to altruism, $\kappa < \phi(1 - \phi)$, and low costs of mobility. Parameter values: $\kappa = 0.15$ and $\nu = 0.01$. *B*, Stochastic trajectories. Average of 10 stochastic simulations (*continuous curve*) and deterministic approximation (*dashed curves*). Parameter values as in *A*. *C*, Divergence to more altruism under low cost sensitivity to altruism and high costs of mobility. Parameter values: $\kappa = 0.1$ and $\nu = 0.1$. *D*, Stochastic trajectories. Parameter values as in *C*. Filled circles indicate attractive ESSs. Arrows give the direction of evolution. Mutation parameters: $k = 0.01$ and $\sigma = 0.05$ in *B* and $\sigma = 0.01$ in *D*. Other parameter values as in figure 2. Evolutionary isoclines as in figure 3.

tants characterized by a significant degree of altruism will eventually arise by chance and displace the selfish resident (fig. 3C). Therefore, the evolutionary trajectory will sooner or later take off from $(m^*, 0)$. It can be seen numerically that the minimum value of mutant altruism required for invading the selfish resident increases as m^* increases. Thus, according to equation (8), the waiting time for altruism to evolve is shorter as the cost of mobility or habitat connectivity increases or in species with a smaller birth rate (fig. 3C).

Only in the case of a linear pattern of altruism cost may selfishness always be uninvadable, provided that the altruism cost parameter κ is large (not shown) or that both κ and the mobility cost ν are small (fig. 4A, 4B). Under such conditions, altruism may initially rise through small mutational steps, if the ancestral state is not too mobile. Yet at some point in the population's evolutionary history, the trajectory of altruism reverts and eventually heads back to the selfish state, homing in at the mobility ESS m^* where no mutant can invade (results not shown). In contrast, if

κ is small and ν is large enough, selfishness is readily displaced by altruism even through infinitesimal mutations as a result of selection for lower mobility (fig. 4C, 4D). Thus, the cost of mobility has a major impact on the origin of altruism, either determining whether the displacement of selfishness is possible (linear costs of altruism) or affecting the timescale over which altruism evolves (decelerating costs of altruism).

Evolutionary Trajectories of Social Traits

Once the evolutionary rise of altruism from a selfish and highly mobile ancestor is initiated, the assumption of an accelerating cost of altruism becomes more realistic (Le Galliard et al. 2003). Then all possible evolutionary dynamics unfold along a continuum bounded by two archetypal templates, each involving two distinctive evolutionary phases.

One evolutionary template applies to species with a slowly accelerating cost of altruism (low κ and γ close to 1). This template involves a first evolutionary phase characterized by the evolutionary reduction of mobility, while altruism shows little change; at the same time, local aggregation is enhanced (fig. 5A–5C). During the second phase, altruism rises along with some increase in mobility (fig. 5C). How this second phase ends depends on the cost of mobility. In the case of a high cost of mobility, the evolutionary trajectory simply heads to the ESS (which is a stable-node equilibrium). In the case of a moderate cost of mobility, the eco-evolutionary feedback causes damped oscillations of the adaptive traits around the ESS (a stable-focus equilibrium; fig. 5A, 5B). Notice that evolution to the extinction boundary can preclude convergence to the ESS (fig. 5B).

The other evolutionary template applies to species with rapidly accelerating costs of altruism (fig. 5D–5F). During the first phase of the evolutionary dynamics, the degree of altruism rises while mobility and the level of local aggregation remain essentially constant. The second phase drives the system to the ESS and is characterized by a marked decrease in mobility, possibly along with a further increase in altruism, while local aggregation is enhanced significantly (fig. 5F). In this scenario, the ES altruism rate is usually low.

Evolutionarily Induced Correlations between Altruism and Mobility

Physiological, life-history, or environmental change can cause the ES traits to co-vary. The conventional wisdom is that selected altruism and selected mobility should correlate negatively across populations or species. Here, we analyze patterns of altruism and mobility covariation in

species characterized by accelerating costs of altruism, in response to underlying changes in life history (birth and death rates) or in constraints on mobility (habitat connectivity and cost of mobility).

Univariate changes in life-history traits (b or d) lead to a negative correlation between the two adaptive traits at evolutionary equilibrium: less altruism and more mobility are selected for in longer-lived or less fecund species (fig. 6A, 6B). However, except in species that are characterized by low fecundity (small b) and low cost of altruism (small κ), the quantitative effect is weak and unlikely to be amenable to empirical detection. In contrast, changes in constraints on mobility (n and ν) can result in an unexpected positive correlation between selected altruism and selected mobility (fig. 6C, 6D). This correlation pattern is more pronounced for species with slowly accelerating costs of altruism and with costs of mobility spanning a range that excludes extremely high and low values (fig. 6D, *continuous curve*).

These qualitative patterns can be understood by considering the selective feedbacks and interactions governing the evolution of both adaptive traits (fig. 1). The intrinsic birth rate b influences the evolution of mobility and altruism via an effect on local aggregation (app. B). As b increases, local aggregation increases, selecting for higher mobility and altruism. The intrinsic death rate d has a direct positive effect on relatedness and a negative effect via local aggregation (eq. [6]): in total, as d increases, relatedness decreases, selecting for less altruism. Increasing the intrinsic death rate d has also a negative effect on mobility via local aggregation and the conversion factor of the selective pressure for mobility (eq. [4]), thus selecting for less mobility. However, as b and d increase, the change in mobility affects local aggregation, opposing the change in altruism. The negative correlation between u^* and m^* represents the net effect of these influences acting altogether when b or d vary independently.

Variation in n or ν may reflect different environmental constraints on individual mobility. A larger value of n causes a rise in the discounting factor of kin cooperation benefits (eq. [5]) and reduces habitat saturation, which decreases both relatedness and the marginal gain in open space from mobility (eq. [4]). Increasing habitat connectivity n therefore weakens the selective pressure for both traits and causes their joint adaptive decline. Increasing the cost of mobility ν over a range that excludes very high and very low values promotes the evolution of significantly higher altruism (for the cost of mobility is not too low), which causes a marked increase of local aggregation. Higher local aggregation in turn exerts a selective pressure for mobility, which exceeds the accrued cost of mobility (for the cost of mobility is not too high). Thus, the selective

interaction between altruism and mobility underlies the joint rise of altruism and mobility at the ESS (fig. 6D).

Discussion

We have used spatial invasion fitness to analyze the joint evolutionary dynamics of altruism and mobility, thereby introducing a unifying framework for investigating the evolution of social traits. Following Perrin and Lehmann (2001), this allowed us to integrate two previously separate lines of research that are focusing, respectively, on altruism evolution under fixed mobility and on mobility evolution under fixed altruism.

Joint Evolution versus Single-Trait Evolution

Our analysis has revealed a variety of phenomena that are obscured from recognition unless altruism and mobility are permitted to evolve jointly. First, evolutionary trajectories on higher-dimensional adaptive landscape can bypass fitness valleys that are insuperable by single-trait evolution. In our study, this general finding applies to the repelling evolutionary isoclines of altruism in figures 4C, 4D, 5A, and 5B: ancestral states below these isoclines could never evolve toward higher degrees of altruism were it not for the concomitant evolution of mobility. For example, when costs of altruism are linear and low, a selfish and sufficiently mobile ancestor will always be uninvadable if mobility is fixed (fig. 4C, 4D; see also Le Galliard et al. 2003). In contrast, if mobility is allowed to evolve and its cost is high enough, selfishness will be readily displaced, even through infinitesimal mutational steps. A similar conclusion applies in figure 5A and 5B. Joint evolution, however, may sometimes also obstruct the evolution of altruism. When costs of mobility and altruism are low and the latter is linear, altruism will increase if mobility is fixed at low levels, whereas joint evolution concomitantly increases mobility, which eventually drives the population back to selfishness.

The joint evolution also affects the evolution of mobility. Mobility is favored by the selective pressure to open space for mutants during invasion and is opposed by physiological costs. The strength of the former pressure is directly and indirectly (through local aggregation) modulated by the degree of altruism. More altruism weakens that selective pressure, as expected from the benefits of philopatry in social species (Stacey and Ligon 1991). However, and less intuitively, selection for more mobility occurs as a result of more altruism enhancing local aggregation. When both traits evolve, this synergistic selective interaction between mobility and altruism affects species with slowly

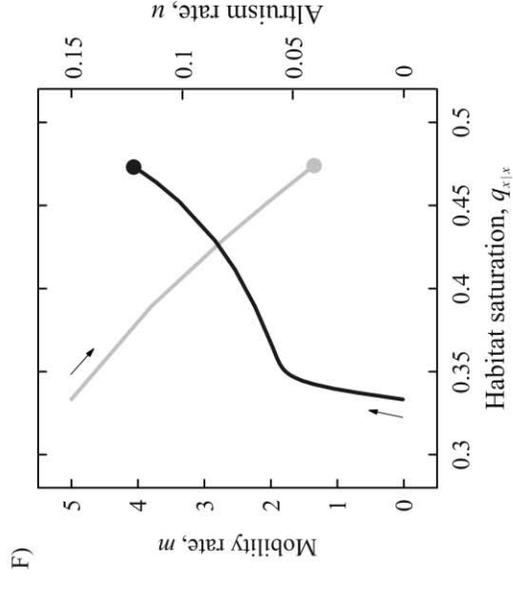
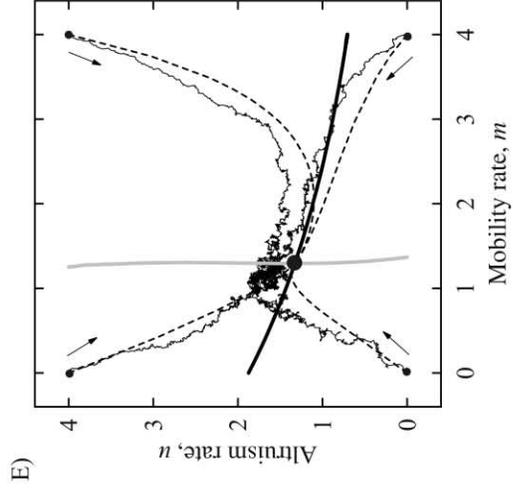
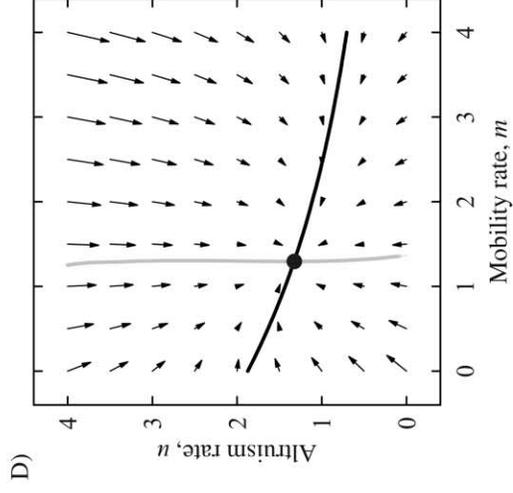
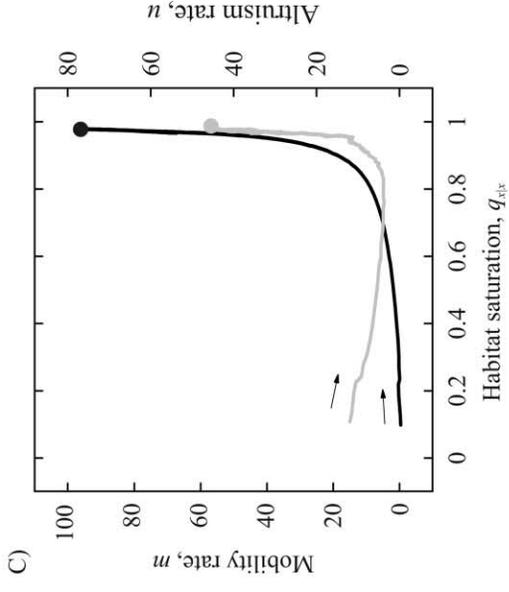
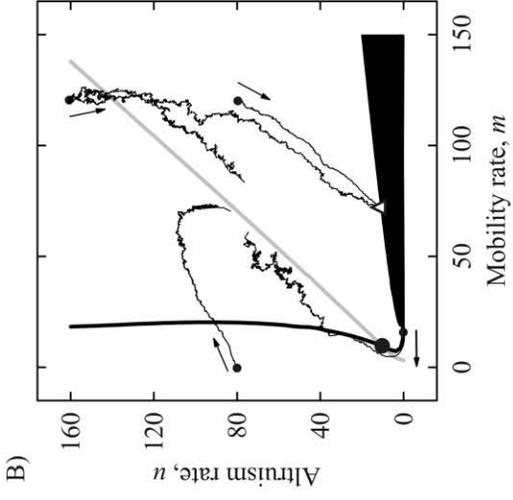
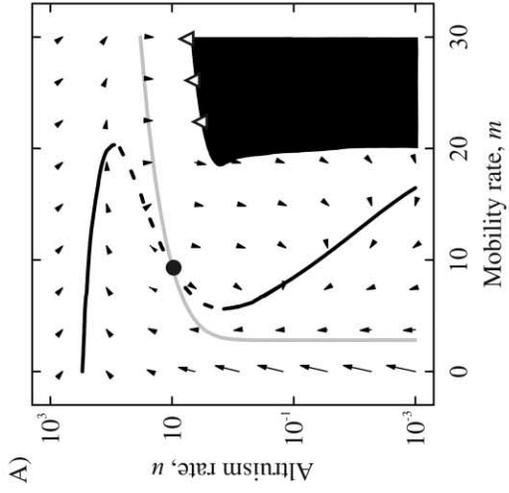
accelerating costs of altruism and moderate costs of mobility (see fig. 5A). In such species, mobility selected through the joint evolutionary process can be considerably higher than that predicted in a selfish species and considerably lower than that predicted in a highly altruistic species. Thus, neglecting the propensity for altruism to co-evolve with mobility can lead to underestimating or overestimating the level of mobility favored by natural selection.

The bidimensionality of the trait space also has a marked effect on the evolutionary dynamics of altruism when the physiological cost is slowly accelerating. In this case, the strong evolutionary attractiveness of the mobility rate that maximizes fitness for intermediate degrees of altruism suffices to transform evolutionary singularities that are repelling with respect to altruism into attractive singularities. The joint ESS for altruism and mobility still bears the footprint of the one-dimensional instability for altruism: this ESS behaves as a focus, causing evolutionary trajectories to spiral around it. Hence, even if populations originate in the same ancestral state and share the same physiological, demographic, and ecological features, they will display high and low levels of mobility and altruism (in all four possible combinations) should they be observed at different epochs of their evolutionary history. This is yet another historical effect that could elucidate comparative analyses confronting a lack of regularity in patterns of social traits and potential correlates (Arnold and Owens 1999).

Correlative Patterns of Social Traits

Habitat saturation models predict that, at evolutionary equilibrium, altruism and mobility should correlate negatively and that more altruism, hence less mobility, should be observed in populations characterized by stronger constraints on dispersal or by lower mortality (Perrin and Lehmann 2001). Our analysis, however, clearly shows that evolutionary outcomes cannot be predicted solely from the effect of habitat saturation and its hypothesized underlying ecological or demographic determinants. This is because habitat saturation is a dynamic variable entangled in the eco-evolutionary feedbacks involving altruism and mobility, the adaptive change of either trait also has a direct effect on the selective pressure influencing the other trait, and life-history traits (birth and death rates) have effects on the evolutionary dynamics independently of their influence on habitat saturation.

We find that selected altruism correlates positively with the cost of mobility and negatively with habitat connectivity. We also predict a positive correlation between selected altruism and mobility in response to changes in



habitat connectivity or in the cost of mobility within a range that excludes extremely low and high values. These results can be compared with those obtained by Perrin and Lehmann (2001), who investigated the joint evolution of altruism and natal dispersal. Their kin selection model differs from ours in three crucial aspects: the habitat is structured into saturated patches of given size, time is discrete and generations do not overlap, and individual behavior is influenced by kin discrimination. Irrespective of the kin discrimination mechanism, their model predicts a negative correlation across populations differing in dispersal cost and a positive correlation across populations differing in patch size. The latter is a consequence of higher relatedness when patches are smaller, which favors both more altruism and more dispersal in their model; exactly the same effects arise in our model when the neighborhood size shrinks. In contrast, our results depart from their finding of a negative correlation in response to increasing the dispersal cost; in our model, such a negative correlation arises only for very low (and very high) values of the mobility cost. This discrepancy might underline a qualitative consequence of the discrimination mechanisms that Perrin and Lehmann (2001) considered (whereas altruism is unconditional in our model), which affects how altruistic benefits are distributed.

Our finding that low habitat connectivity or high cost of mobility selects for more altruism suggests that comparative studies should find consistent relationships between physiological and habitat constraints on dispersal and levels of cooperation. Some recent intraspecific comparisons in vertebrates reported a negative effect of habitat connectivity on investment in helping (e.g., Spinks et al. 2000; Russell 2001). Also, in the group of African mole rats (Bathyergidae), cooperative breeding has been linked to the scarce and heterogeneous distribution of resources in arid landscapes, which results in high costs of mobility (Jarvis et al. 1994). In agreement with our findings, the comparative analysis of sociality (as measured by reproductive skew) yields a rough correlation between costs of mobility and cooperation, with the eusocial species culminating in correspondence with the most arid environment (Faulkes and Bennett 2001).

Empirical data relating altruism and mobility are scant, especially because quantitative assessments of dispersal in social and asocial species are difficult to obtain. Comparative analyses of social traits in birds are still insufficient to test our prediction that more cooperation could be associated with higher levels of mobility as an adaptive response to ecological constraints. However, the observation by Arnold and Owens (1999) that the correlation patterns between dispersal and cooperative breeding depend on the taxonomic level warrants further analyses. The occurrence of a dispersing morph in the eusocial naked mole rat *Heterocephalus glaber* could also be the manifestation of an adaptive association between strong altruism and dispersal ability (O’Riain et al. 1996). The fact that this dispersing morph participates little in cooperative activities further suggests that constraints on mobility might lead to a stable genetic polymorphism of selfish-mobile and altruistic-sessile phenotypes or to adaptive developmental plasticity. Although the evolution of polymorphism was not observed in our study, it was first hypothesized by van Baalen and Rand (1998) and has been reported in cellular automaton models involving regular lattices (Koella 2000).

We predict life-history traits (birth and death rates) to have, in isolation, little influence on the selected combination of altruism and mobility. On the one hand, an increase in the intrinsic birth rate drives a decrease in altruism and an increase in mobility, although the predicted pattern is fairly flat and probably difficult to detect in real data. On the other hand, more altruism evolves among species with the highest mortality rates. This finding conflicts with the main conclusion of Taylor and Irwin (2000) and Irwin and Taylor (2001) that altruism is more strongly favored in response to lower mortality. In fact, the models by Taylor and Irwin show primarily that lower mortality increases relatedness between altruists, an effect that is also found in this model. Our analysis emphasizes, however, that net effect of decreasing mortality on the whole web of eco-evolutionary feedback and selective interaction is to promote less altruism and more mobility.

On the empirical end, comparative analyses in birds have attempted to relate social behavior with nestling mor-

Figure 5: Joint evolution of altruism and mobility with an accelerating cost of altruism. *A*, Convergence to a stable focus under slowly accelerating costs of altruism and intermediate costs of mobility. Parameter values: $\gamma = 1.2$, $\kappa = 0.05$, and $\nu = 0.05$. *B*, Stochastic trajectories. Trajectories differ quantitatively from the deterministic approximation but remain qualitatively similar in this case. Finite population size and random mutational steps induce contingency: starting from the same mobile, altruistic ancestor, trajectories can either converge to the focus or collide with the extinction boundary (*triangle*). *C*, Relationship between local aggregation and mobility (*gray curve*) or altruism (*black curve*) in the course of adaptive evolution (*arrows*) from stochastic trajectories. Parameter values as in *A*. *D*, Convergence to a stable node under rapidly accelerating costs of altruism. Parameter values: $\gamma = 2$, $\kappa = 0.05$, and $\nu = 0.1$. *E*, Stochastic trajectories. Parameter values as in *D*. *F*, Relationship between local aggregation and mobility (*gray curve*) or altruism (*black curve*) in the course of adaptive evolution (*arrows*). Parameter values as in *D*, except $\kappa = 0.5$. Mutation parameters: $k = 0.01$ and $\sigma = 0.01$. Filled circles indicate attractive ESSs. Arrows show the selection gradients. Dark areas indicate population extinction. Other parameter values as in figure 2. Evolutionary isoclines as in figure 3.

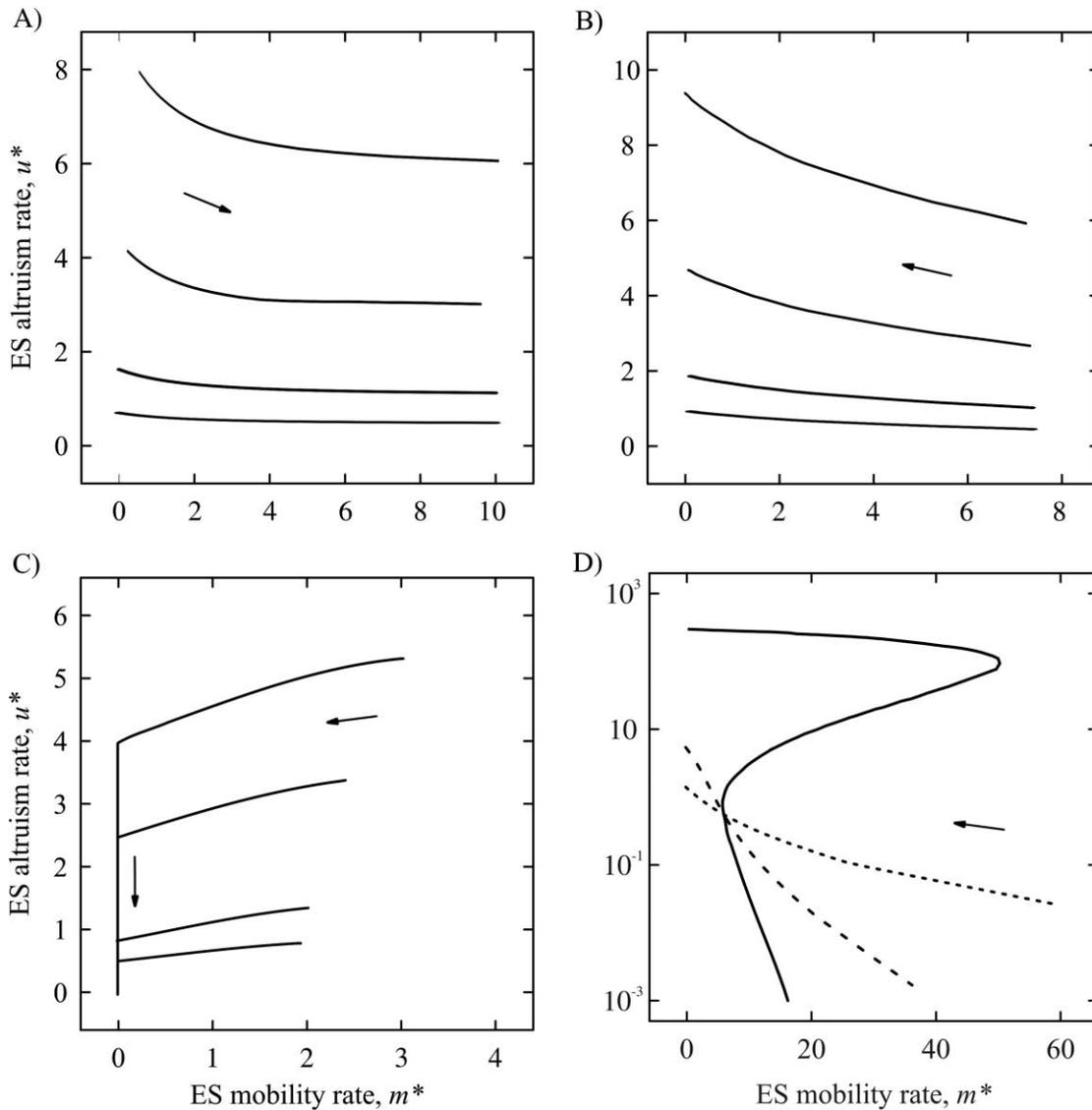


Figure 6: Correlations between altruism and mobility induced by evolution with accelerating costs of altruism. Arrows indicate the effect of increasing the parameter value. A, Effect of varying the birth rate, b , for different values of the cost parameter κ . Parameter values: $\gamma = 2$ and $\nu = 0.1$. B, Effect of varying the death rate, d , for different values of κ . Parameter values: $\gamma = 2$, $\nu = 0.1$, and $b = 6$. In A and B, $\kappa = 0.01$, $\kappa = 0.02$, $\kappa = 0.05$, and $\kappa = 0.1$ from top to bottom. C, Effect of habitat connectivity, n , for different values of κ . Parameter values: $\gamma = 2.5$ and $\nu = 0.1$. From top to bottom: $\kappa = 0.005$, $\kappa = 0.01$, $\kappa = 0.05$, $\kappa = 0.1$. D, Effect of the cost of mobility, ν , for different levels of cost acceleration: $\gamma = 1.2$ (continuous curve, results from stochastic simulations), $\gamma = 1.5$ (dashed curve), $\gamma = 2$ (dotted curve). Parameter values: $\kappa = 0.05$. Other parameters as in figure 2.

tality and adult mortality (Hatchwell and Komdeur 2000). It was found that nestling mortality had no detectable influence on the distribution of social characters (Poiani and Pagel 1997), in agreement with our prediction that the intrinsic birth rate (which can be seen as combining fecundity and offspring mortality) is likely to have undetectable effects. The analysis of the whole available phy-

logeny of birds yields a pattern of stronger cooperation along with lower adult mortality (Arnold and Owens 1998). This empirical pattern supports our finding of an effect of the death rate but contradicts the direction that we predict. The pattern could be recovered in our model, however, under the assumption that lower mortality trades off across species with lower fecundity, which is known to

occur in birds (Arnold and Owens 1998). This suggests that covariation of life-history traits is important to consider when investigating the determinants of patterns of social traits.

The Habitat Saturation Hypothesis

Our analysis supports the view that habitat saturation is a critical nexus in the selective interaction between altruism and mobility (Emlen 1982, 1994; Koenig et al. 1992). The habitat saturation hypothesis states that constraints on independent breeding favor philopatry and helping and provides a fruitful approach to the evolution of social traits from the empirical end. Our theory leads to reexamining the basis and scope of this hypothesis and clarifies the selective pathways whereby habitat saturation influences and becomes influenced by the evolution of social traits.

Habitat saturation has long been regarded as a key to the evolution of social behavior. This hypothesis was originally put forward to explain the evolution of cooperative breeding in birds (Brown 1978; Emlen 1982) and is now underlying theories for the evolution of delayed dispersal and reproductive skew (Reeve et al. 1998; Kokko and Lundberg 2001). The general view is that habitat saturation drives the joint evolution of philopatry and altruism (Perrin and Lehmann 2001). By offering an explicit mathematical framework to deal with the interplay of social behavior and population dynamics, our analysis deciphers the selective pathways whereby habitat saturation is involved in the evolution of social traits.

The habitat saturation hypothesis assumes that sociality evolves in two steps: the evolution of philopatry at first and, next, the evolution of cooperation (Helms Cahan et al. 2002). As habitat saturation increases, floating and queuing before gaining access to a territory induce strong costs of dispersal. This favors delayed dispersal, which would set the condition for the cost of local crowding to be ameliorated by cooperating rather than simply competing (Kokko and Lundberg 2001). What causes habitat saturation in the first place? The scenario of “ecological constraints” asserts that environmental factors constrain mobility to low levels, hence local crowding. Such environmental factors may involve habitat structure, physical predicaments to movement, or a large physiological cost of moving (Jarvis et al. 1994; Russell 2001). The life-history hypothesis assumes that habitat saturation is more likely to occur in species with low mortality, in which the turnover of breeding sites would be slow (Arnold and Owens 1998).

Our analysis highlights a rather different evolutionary scenario. First, there are two distinct components to habitat saturation, which play complementary roles in the evolution of social traits. “Local aggregation” $\bar{q}_{x|x}$ measures

habitat saturation around individuals, in line with the original definition of habitat saturation by Emlen (1982). “Local contention” $\bar{q}_{x|0}$ measures habitat saturation around vacant sites; it is directly related to the degree of clustering of vacant sites ($\bar{q}_{0|0} = 1 - \bar{q}_{x|0}$) and thus measures how isolated groups of occupied sites are. Like in the ecological constraints scenario, a high cost of dispersal and low habitat connectivity are important determinants of the evolution of local aggregation and local contention. However, our model emphasizes that habitat saturation is a consequence of the evolution of low mobility rather than the primary selective factor for that evolution. In other words, philopatry is an adaptive response to environmental constraints and physiological costs rather than to habitat saturation per se.

In fact, neither local aggregation nor local contention is maximized during the joint evolution of altruism and mobility. In single-trait evolution, however, the mobility rate evolves such as to maximize local contention—a prediction qualitatively similar to the finding that the number of competitors for territories (the limiting resource) is typically maximized by the evolution of habitat choice strategies (Kokko et al. 2001). Yet this remarkable principle evaporates when altruism evolves concomitantly with mobility. Furthermore, the evolution of low mobility and strong aggregation does not appear as an obligate evolutionary step toward sociality. The model presented here uncovers an alternative scenario according to which a population initiated in the selfish and highly mobile ancestral state first evolves a substantial degree of altruism, while aggregation remains low, before adaptive evolution secondarily favors reduced mobility, which may in turn lead to strong aggregation.

One key feature of our analysis is that habitat saturation is treated not as a fixed parameter but as a pair of dynamical variables that close the eco-evolutionary feedback loops entangling altruism and mobility. Local aggregation and local contention, respectively, are the pivotal factors of the two eco-evolutionary feedback loops linking altruism and mobility. When both traits evolve jointly, local aggregation turns out to be the dominant mediator of the selective interaction between them. Local aggregation responds antagonistically to evolutionary change of altruism and mobility, which in turn affects the selective pressures acting on both traits. Such essential eco-evolutionary feedbacks and selective interactions have been ignored in most previous models of social evolution (but see Kokko and Lundberg 2001).

The dynamical nature of local aggregation and contention in our model results from the stochastic nature of the demographic process and especially from the site opening process generated by individual mortality. The numerical model of Mitteldorf and Wilson (2000) also

showed that population elasticity, that is, variable local density, can facilitate the evolution of altruism, even when generations do not overlap. In Nakamaru et al.'s (1997, 1998) models, the availability of empty space was also a critical feature for the spread of cooperation. These authors further emphasized the consequences of assuming survival altruism rather than reproduction altruism. In the latter case (which is considered here), the evolution of social traits affects the birth rate and, therefore, does not influence the site opening process, driven by mortality. If altruism impacts survival, such a feedback could exist. The adaptive increase of altruism would reduce the death rate and hence the rate of site opening; as a consequence, the selective pressure of local competition against altruism would be enhanced. Such a negative effect on the evolution of altruism might be offset, however, would some form of environmental stochasticity drive site opening, insensitive to the evolutionary change of altruism (Mitteldorf and Wilson 2000).

Concluding Remarks

The habitat saturation hypothesis, the ecological constraint model, and the life-history hypothesis represent varied attempts at singling out general factors of social evolution. By integrating some of their key ingredients, our model leads to the conclusion that no simple determinism should be expected for the origin of social behavior or the evolution of strong cooperative interaction. Thus, inferences from studies based on univariate analyses are likely to be hindered by the complexity and diversity of factors involved in the evolution of social traits (Crespi and Choe 1997). However, some general principles hold: physiological or ecological constraints on mobility are essential to explain the origin of altruism; all evolutionary trajectories can be related to only two archetypal, contrasting routes to sociality; patterns of covariation among social traits can be understood as adaptive responses to multivariate changes in life-history traits.

Eco-evolutionary feedbacks and selective interactions are central to the joint evolutionary dynamics of social traits. Taking them into account allowed us to address a hotly debated issue in the biology of social behavior: whether the high relatedness between interacting individuals of several social species predicted by Hamilton's (1964*a*, 1964*b*) kin selection theory is the direct consequence of physiological or ecological constraints on dispersal or the outcome of more involved mechanisms of active assortment, involving communication, cognition, and habitat choice (Hamilton 1975). We offer the alternative view that in some social systems, both limited mobility and strong altruism form the joint adaptive response to a web of multiple, interacting selective mechanisms,

while in other systems, the spatial self-structuring of a population leads to the evolution of high mobility without compromising the likelihood of passive assortment between altruistic partners.

Acknowledgments

We are grateful to L. Lehmann and one anonymous reviewer for comments on an earlier version of this manuscript. This work has been financially supported by the Adaptive Dynamics Network at the International Institute for Applied System Analysis (Laxenburg, Austria); the French Ministry of Research and Education; the Austrian Science Fund; the Austrian Federal Ministry of Education, Science, and Cultural Affairs; and the European Science Foundation's Theoretical Biology of Adaptation Programme. Collaboration on this study has been fostered by the European Research Training Network ModLife (Modern Life-History Theory and Its Application to the Management of Natural Resources), supported by the Fifth Framework Programme of the European Community.

Literature Cited

- Abrams, P. A. 2001. Modelling the adaptive dynamics of traits involved in inter- and intraspecific interactions: an assessment of three methods. *Ecology Letters* 4:166–175.
- Arnold, K. E., and I. P. F. Owens. 1998. Cooperative breeding in birds: a comparative test of the life-history hypothesis. *Proceedings of the Royal Society of London B* 265:739–745.
- . 1999. Cooperative breeding in birds: the role of ecology. *Behavioral Ecology* 10:465–471.
- Brown, J. L. 1978. Avian communal breeding systems. *Annual Review of Ecology and Systematics* 9:123–155.
- Choe, J. C., and B. J. Crespi. 1997. *The evolution of social behavior in insects and arachnids*. Cambridge University Press, Cambridge.
- Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296:69–72.
- Clutton-Brock, T. H., D. Gaynor, R. Kansky, A. D. C. MacColl, G. McIlrath, P. Chadwick, P. N. M. Brotherton, J. M. O'Riain, M. Manser, and J. D. Skinner. 1998. Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proceedings of the Royal Society of London B* 265:185–190.
- Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics* 29:141–177.
- Cohen, D., and U. Motro. 1989. More on optimal rates of dispersal: taking into account the cost of dispersal mechanism. *American Naturalist* 134:659–663.
- Crespi, B. J. 2001. The evolution of social behavior in microorganisms. *Trends in Ecology & Evolution* 16:178–183.
- Crespi, B. J., and J. C. Choe. 1997. Explanation and evolution of social systems. Pages 499–524 in J. C. Choe and B. J. Crespi, eds. *The evolution of social behavior in insects and arachnids*. Cambridge University Press, Cambridge.
- Day, T., and P. D. Taylor. 1998. Unifying genetic and game theoretic models of kin selection for continuous traits. *Journal of Theoretical Biology* 194:391–407.

- Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology* 34:579–612.
- Dieckmann, U., R. Law, and J. A. J. Metz. 2000. The geometry of ecological interactions: simplifying spatial complexities. Cambridge University Press, Cambridge.
- Ellner, S. P., A. Sasaki, Y. Haraguchi, and H. Matsuda. 1998. Speed of invasion in lattice population models: pair-edge approximation. *Journal of Mathematical Biology* 36:469–484.
- Emlen, S. T. 1982. The evolution of helping. I. An ecological constraints model. *American Naturalist* 119:29–39.
- . 1994. Benefits, constraints and the evolution of family. *Trends in Ecology & Evolution* 9:282–285.
- . 1997. Predicting family dynamics in social vertebrates. Pages 228–253 in J. R. Krebs and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. Blackwell Science, Oxford.
- Eshel, I. 1983. Evolutionary and continuous stability. *Journal of Theoretical Biology* 103:99–111.
- Faulkes, C. G., and N. C. Bennett. 2001. Family values: group dynamics and social control of reproduction in African mole-rats. *Trends in Ecology & Evolution* 16:184–190.
- Ferrière, R., and J.-F. Le Galliard. 2001. Invasion fitness and adaptive dynamics in spatial population models. Pages 57–79 in J. Clobert, E. Danchin, A. A. Dhondt, and J. Nichols, eds. *Dispersal*. Oxford University Press, Oxford.
- Frank, S. A. 1995. Mutual policing and repression of competition in the evolution of cooperative groups. *Nature* 377:520–522.
- . 1998. *Foundations of social evolution: monographs in behavior and ecology*. Princeton University Press, Princeton, NJ.
- Geritz, S. A. H., E. Kisdi, G. Meszena, and J. A. J. Metz. 1998. Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12:35–57.
- Gillespie, D. T. 1976. A general method for numerically simulating the stochastic time evolution of coupled chemical reactions. *Journal of Computational Physics* 22:403–434.
- Grafen, A. 1984. Neutral selection, kin selection, and group selection. Pages 62–84 in J. R. Krebs and N. B. Davies, eds. *Behavioral ecology*. Blackwell, Oxford.
- Hamilton, W. D. 1964a. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7:1–16.
- . 1964b. The genetical evolution of social behaviour. II. *Journal of Theoretical Biology* 7:17–52.
- . 1975. Innate social aptitudes of man: an approach from evolutionary genetics. Pages 133–155 in R. Fox, ed. *Biosocial anthropology*. Wiley, New York.
- Harada, Y., and Y. Iwasa. 1994. Lattice population dynamics for plants with dispersing seeds and vegetative propagation. *Researches on Population Ecology* 36:237–249.
- Hatchwell, B. J., and J. Komdeur. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour* 59:1079–1086.
- Helms Cahan, S., D. T. Blumstein, L. Sundström, L. Liebig, and A. Griffin. 2002. Social trajectories and the evolution of social behaviour. *Oikos* 96:206–216.
- Irwin, A. J., and P. D. Taylor. 2001. Evolution of altruism in stepping-stone populations with overlapping generations. *Theoretical Population Biology* 60:315–325.
- Jarvis, J. U. M., M. J. O’Riain, N. C. Bennett, and P. W. Sherman. 1994. Mammalian eusociality: a family affair. *Trends in Ecology & Evolution* 9:47–51.
- Kelly, J. K. 1994. The effect of scale dependent processes on kin selection: mating and density regulation. *Theoretical Population Biology* 46:32–57.
- Koella, J. 2000. The spread of altruism versus the evolutionary response of egoists. *Proceedings of the Royal Society of London B* 267:1979–1985.
- Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, and M. T. Stanback. 1992. The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* 67:111–150.
- Kokko, H., and P. Lundberg. 2001. Dispersal, migration, and offspring retention in saturated habitats. *American Naturalist* 157:188–202.
- Kokko, H., W. J. Sutherland, and R. A. Johnstone. 2001. The logic of territory choice: implications for conservation and source-sink dynamics. *American Naturalist* 157:459–463.
- Le Galliard, J.-F., R. Ferrière, and U. Dieckmann. 2003. The adaptive dynamics of altruism in spatially heterogeneous populations. *Evolution* 57:1–17.
- Marrow, P., U. Dieckmann, and R. Law. 1996. Evolutionary dynamics of predator-prey systems: an ecological perspective. *Journal of Mathematical Biology* 34:556–578.
- Matsuda, H., N. Ogita, A. Sasaki, and K. Sato. 1992. Statistical mechanics of population: the lattice Lotka-Volterra model. *Progress of Theoretical Physics* 88:1035–1049.
- Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define fitness for general ecological scenarios? *Trends in Ecology & Evolution* 7:198–202.
- Michod, R. E. 1999. *Darwinian dynamics: evolutionary transitions in fitness and individuality*. Princeton University Press, Princeton, NJ.
- Mitteldorf, J., and D. S. Wilson. 2000. Population viscosity and the evolution of altruism. *Journal of Theoretical Biology* 204:481–496.
- Morris, A. 1997. Representing spatial interactions in simple ecological models. PhD diss. University of Warwick, Coventry.
- Nakamaru, M., H. Matsuda, and Y. Iwasa. 1997. The evolution of cooperation in a lattice-structured population. *Journal of Theoretical Biology* 184:65–81.
- Nakamaru, M., H. Nogami, and Y. Iwasa. 1998. Score-dependent fertility model for the evolution of cooperation in a lattice. *Journal of Theoretical Biology* 194:101–124.
- O’Riain, M. J., J. U. M. Jarvis, and C. G. Faulkes. 1996. A dispersive morph in the naked mole-rat. *Nature* 380:619–621.
- 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. *American Naturalist* 158:471–483.
- Poiani, A., and M. Pagel. 1997. Evolution of avian cooperative breeding: comparative tests of the nest predation hypothesis. *Evolution* 51:226–240.
- Queller, D. C. 1992. Does population viscosity promote kin selection? *Trends in Ecology & Evolution* 7:322–324.
- Rand, D. 1998. Correlation equations and pair approximation for spatial ecologies. Pages 100–143 in J. McGlade, ed. *Advanced ecological theory*. Blackwell Science, Oxford.
- Reeve, H. K., S. T. Emlen, and L. Keller. 1998. Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behavioral Ecology* 9:267–278.
- Russell, A. F. 2001. Dispersal costs set the scene for helping in an

- atypical avian cooperative breeder. *Proceedings of the Royal Society of London B* 268:95–99.
- Spinks, A. C., J. U. M. Jarvis, and N. C. Bennett. 2000. Comparative patterns of philopatry and dispersal in two common mole-rat populations: implications for the evolution of mole-rat sociality. *Journal of Animal Ecology* 69:224–234.
- Stacey, P. B., and J. D. Ligon. 1991. The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. *American Naturalist* 137: 831–846.
- Taylor, P. D. 1992. Inclusive fitness in a homogeneous environment. *Proceedings of the Royal Society of London B* 249:299–302.
- Taylor, P. D., and A. J. Irwin. 2000. Overlapping generations can promote altruistic behavior. *Evolution* 54:1135–1141.
- Thorne, B. L. 1997. Evolution of eusociality in termites. *Annual Review of Ecology and Systematics* 28:27–54.
- van Baalen, M. 2000. Pair approximation for ecological interactions on different geometries. Pages 359–387 in U. Dieckmann, R. Law, and J. A. J. Metz, eds. *The geometry of ecological interactions: simplifying spatial complexities*. Cambridge University Press, Cambridge.
- van Baalen, M., and D. Rand. 1998. The unit of selection in viscous populations and the evolution of altruism. *Journal of Theoretical Biology* 193:631–648.
- West, S. A., M. G. Murray, C. A. Machado, A. S. Griffin, and E. A. Herre. 2001. Testing Hamilton's rule with competition between relatives. *Nature* 409:510–513.
- Wilson, D. S., G. B. Pollock, and L. A. Dugatkin. 1992. Can altruism evolve in purely viscous populations? *Evolutionary Ecology* 6:331–341.

Associate Editor: Nicolas Perrin

Appendix A from J.-F. Le Galliard et al., “Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility”

(Am. Nat., vol. 165, no. 2, p. 206)

Population Dynamics

We consider a social network comprising a large number of homogeneous sites occupied by a population of mutants, called y , and residents, denoted by x . A mutant y located at a site z on the network experiences the following birth, death, and movement rates:

$$\begin{aligned} b_y(z) &= \left(b + \sum_{j=x,y} \phi u_j n_{j|y}(z) - C(m_y, u_y) \right) \phi n_{0|y}(z), \\ d_y(z) &= d, \\ m_y(z) &= m \phi n_{0|y}(z). \end{aligned} \tag{A1}$$

To derive the dynamics of the mutant’s population size, we average birth and death rates described in equation (A1) over all sites of the network occupied by the mutant, which gives

$$\frac{dN_y}{dt} = [(b - C(m_y, u_y)) \phi E(n_{0|y}(z)) - d] N_y + \sum_{j=x,y} \phi^2 u_j \sum_z n_{j|y}(z) n_{0|y}(z), \tag{A2a}$$

where $E(n_{0|y}(z))$ is the network average of the number of empty sites neighboring a site occupied by a mutant. The third term in equation (A2a) is a product between random variables describing alternative neighborhoods of a mutant individual. Assuming a multinomial probability distribution of sites and independence between the neighborhoods of pairs of sites (Morris 1997), we have

$$\sum_z n_{j|y}(z) n_{0|y}(z) = N_y n(n-1) q_{j|y} q_{0|y}, \tag{A2b}$$

where $q_{k|y}$ is the average local frequency of type k sites neighboring a mutant. The dynamics of the mutant’s population size is then given by

$$\frac{dN_y}{dt} = \left\{ \left[b + \sum_{j=x,y} (1 - \phi) u_j q_{j|y} - C(m_y, u_y) \right] q_{0|y} - d \right\} N_y = \lambda_y N_y, \tag{A2c}$$

which involves the configurations of pairs of sites. A closed system describing the pair dynamics is obtained by Le Galliard et al. (2003) from the bookkeeping of all events affecting pairs of sites:

$$\begin{aligned}
 \frac{dN_{0y}}{dt} &= (\alpha'_y q_{0|0} - \beta_y - \delta_y)N_{0y} + \delta_x N_{xy} + \delta_y N_{yy}, \\
 \frac{dN_{yy}}{dt} &= 2\beta_y N_{0y} - 2\delta_y N_{yy}, \\
 \frac{dN_{xy}}{dt} &= (\alpha_x + \alpha'_y q_{x|0})N_{0y} - (\delta_x + \delta_y)N_{xy},
 \end{aligned}
 \tag{A3}$$

where α_i is the average per capita input rate of a type i individual into a type $0j$ pair with $j \neq i$ ($\alpha_i = \alpha'_i q_{i|0}$), β_i is the average per capita input rate of a type i individual into a type $0i$ pair, and δ_i is the average per capita output rate of a type i individual from a type ij pair (following van Baalen and Rand 1998; see also app. 2 in Le Galliard et al. 2003).

In general, a resident population converges to a unique stable equilibrium spatial structure, which is described in appendix 3 of Le Galliard et al. (2003). The nontrivial population equilibrium is characterized by $\bar{q}_{x|x}$, which satisfies the quadratic equation $[b + u_x(1 - \phi)\bar{q}_{x|x} - C(u_x, m_x)](1 - \bar{q}_{x|x}) - d = 0$, and by $\bar{q}_{0|0} = \delta_x/\alpha'_x$. If b is sufficiently larger than d , the resident population is nonviable when $\Delta < 0$, where Δ denotes the discriminant of the quadratic equation.

Appendix B from J.-F. Le Galliard et al., “Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility”

(Am. Nat., vol. 165, no. 2, p. 206)

Evolutionary Dynamics

Pseudoequilibrium Frequencies

We use the tilde and bar accents to denote the pseudoequilibrium state of the mutant during invasion and the equilibrium state of the resident, respectively. The pseudoequilibrium frequencies $\tilde{q}_{0|y}$, $\tilde{q}_{x|y}$, and $\tilde{q}_{y|y}$ are the steady states of equation (A3) when x is a resident type at ecological equilibrium and y is a rare mutant type, which gives

$$\begin{aligned} (\bar{\alpha}_x + \tilde{\alpha}'_y \bar{q}_{0|0}) \tilde{q}_{0|y} - (\tilde{\delta}_y + \bar{\delta}_x + \tilde{\lambda}_y) \tilde{q}_{x|y} &= 0, \\ 2\tilde{\beta}_y \tilde{q}_{0|y} - (2\tilde{\delta}_y + \tilde{\lambda}_y) \tilde{q}_{y|y} &= 0. \end{aligned} \quad (\text{B1})$$

Since $\tilde{q}_{y|0} \approx 0$ when the mutant is rare, this nonlinear system involves three unknowns ($\tilde{q}_{0|y}$, $\tilde{q}_{x|y}$, and $\tilde{q}_{y|y}$) and two equations. Together with the constraint $\tilde{q}_{0|y} = 1 - \tilde{q}_{x|y} - \tilde{q}_{y|y}$, equations (B1) can thus be used to evaluate the pseudoequilibrium frequencies of the mutant and hence the spatial invasion fitness defined by equation (3).

Pseudoequilibrium Frequencies of a Degenerate Mutant

In general, there is no analytical solution for the pseudoequilibrium frequencies of a mutant. However, assuming a degenerate mutant with the same phenotype as the resident, the nonlinear system (B1) can be solved analytically. The solutions of equations (B1) in this case are $\tilde{q}_{0|y} = \bar{q}_{0|x}$ and $\tilde{q}_{y|y} = \bar{q}_{y|y}$, where the detailed analytical expression for $\bar{q}_{y|y}$ (the relatedness in our model) is given by equation (6).

Selective Pressure on Mobility

The first component of the selection gradient in equation (1) can be approximated by a first-order Taylor expansion of the spatial invasion fitness with respect to m . Considering a slightly different mobility phenotype $m_y = m_x + \varepsilon$ and the first-order approximations $\tilde{q}_{0|y} = \bar{q}_{0|x} + a\varepsilon$ and $\tilde{q}_{y|y} = \bar{q}_{y|y} + b\varepsilon$ leads to

$$\left. \frac{\partial s_x(y)}{\partial m_y} \right|_{m_y=m_x} = \bar{q}_{0|x} \left\{ \left[\frac{d}{\bar{q}_{0|x}^2} - (1 - \phi)u_x \right] a - \left. \frac{\partial C(m_y, u_x)}{\partial m_y} \right|_{m_y=m_x} \right\} + o(\varepsilon). \quad (\text{B2})$$

The analytical evaluation of a using equations (B1) yields a complicated term affected directly by the mobility and altruism rate, death rate, cost of mobility, and neighborhood size but also indirectly by the effects of all model parameters on the habitat saturation statistics $\bar{q}_{x|x}$ and $\bar{q}_{0|0}$. Numerical sensitivity analyses of the selection components over a large range of parameter values indicate that a is primarily sensitive to changes in mobility rates through local contention $\bar{q}_{x|0}$, with a negative feedback of m on this selection component. For example, assuming a zero mobility cost, local aggregation becomes independent of mobility, whereas local contention increases monotonically with the mobility rate; thus, in this case, the eco-evolutionary feedback on mobility is mediated entirely by local contention and not by local aggregation. The conversion term (expression in brackets in front of a) is primarily sensitive to changes in altruism rate, life-history traits, and habitat structure.

Selective Pressure on Altruism

The second component of the selection gradient can be approximated by a first-order Taylor expansion of the spatial invasion fitness with respect to u . Assuming a slightly deviant mutant $u_y = u_x + \varepsilon$, $\tilde{q}_{0|y} = \bar{q}_{0|x} + a'\varepsilon$, and $\tilde{q}_{y|y} = \bar{q}_{y|y} + b'\varepsilon$, the first-order approximation results in the following expression (see also eq. [3] in Le Galliard et al. 2003):

$$\left. \frac{\partial s_x(y)}{\partial u_y} \right|_{u_y=u_x} = \bar{q}_{0|x} \left\{ (1 - \phi) \bar{q}_{y|y} + \left[\frac{d}{\bar{q}_{0|x}^2} - (1 - \phi) u_x \right] a' - \left. \frac{\partial C(m_x, u_y)}{\partial u_y} \right|_{u_y=u_x} \right\} + o(\varepsilon). \quad (\text{B3})$$