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The evolution of self-fertilization in density-regulated populations

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The evolution of selfing in hermaphrodites has been studied to reveal the demographic conditions that lead to intermediate selfing rates. Using a demographic model based on Ricker-type density regulation, we assume first that, independent of population density, inbred individuals survive less well than outbred individuals and second, that inbred and outbred individuals differ in their competitive abilities in density-regulated populations. The evolution of selfing, driven by inbreeding depression and the cost of outcrossing, is then analysed for three fundamentally different demographic scenarios: stable population densities, deterministically varying population densities (resulting from cyclical or chaotic population dynamics) and stochastic fluctuations of carrying capacities (resulting from environmental noise). We show that even under stable demographic conditions evolutionary outcomes are not confined to either complete selfing or full outcrossing. Instead, intermediate selfing rates arise under a wide range of conditions, depending on the nature of competitive interactions between inbred and outbred individuals. We also explore the evolution of selfing under deterministic and stochastic density fluctuations to demonstrate that such environmental conditions can evolutionarily stabilize intermediate selfing rates. This is the first study, to our knowledge, to consider in detail the effect of density regulation on the evolution of selfing rates.

Keywords: self-fertilization; adaptive dynamics; inbreeding depression; density- and frequency-dependent selection

1. INTRODUCTION

The evolution of self-fertilization has been a focus of interest in evolutionary biology and is considered as being driven by both ecological and genetic factors (Uyenoyama *et al.* 1993). Although widespread in plants, hermaphroditism also exists in animals (Jarne & Charlesworth 1993), underlining the role of selfing as a fundamental genetic system of sexual reproduction. Explanations for the evolution of selfing are based on the dynamics of selfing genes: Fisher (1941) was the first to point out that a gene causing selfing will experience a twofold gain in transmission, compared with a gene causing outcrossing. However, this strong selective advantage of selfing (resulting in a cost of outcrossing) is counteracted by the tendency of selfed progeny to have reduced fitness owing to increased levels of homozygosity (inbreeding depression; Charlesworth & Charlesworth 1987). The balance between these two antagonistic selection pressures is key to the evolution of selfing in hermaphrodites. However, models incorporating both selection pressures predict that complete selfing or full outcrossing are the only two evolutionarily stable selfing rates that can result from this balance (Lloyd 1979; Lande & Schemske 1985; Charlesworth *et al.* 1990; some exceptions based on ecological mechanisms like dispersal limitation or pollen discounting are reviewed in Uyenoyama *et al.* (1993)). Such results conspicuously contrast with empirical observations that demonstrate a high diversity of intermediate selfing rates, in particular in plants (Barrett *et al.* 1996).

One limitation of previous models is their simplified treatment of population dynamics. However, it is obvious that inbreeding depression lowers population growth rates and must thus be expected to impact on population dynamics (Halley & Manasse 1993; Saccheri *et al.* 1998). Moreover, empirical evidence indicates that competitive interactions can modify the magnitude of inbreeding depression, an effect that has so far remained unexplored in theoretical studies. Darwin (1876) observed that the relative height of selfed plants in many plant species decreases with the presence of competitors. This pattern of competitive interaction has recently been confirmed in many taxa, including house mice (Meagher *et al.* 2000), *Drosophila* (Bijlsma *et al.* 1999) and plants (Schmitt & Ehrhardt 1990; Wolfe 1993; Cheptou *et al.* 2000). Moreover, studies on *Drosophila* have demonstrated that competitive ability is the one component of fitness that is most severely affected by inbreeding (Lynch & Walsh 1998).

Although much studied elsewhere in theoretical ecology (Tilman 1988), the consequences of competitive interactions have not been incorporated in models dealing with inbreeding depression (see, however, Lloyd (1980)). As population density may influence the severity of inbreeding depression, it can, in turn, modify the selective advantage of selfing. This realization has led Uyenoyama *et al.* (1993) to emphasize the necessity of accounting for demographic details and competitive interactions in future models for the evolution of selfing.

In this paper, we construct a general demographic model for hermaphrodites and employ it to study the evolution of selfing. Based on Ricker-type density regulation (May & Oster 1976), the fitness of inbred and out-

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bred progeny is derived as a function of the underlying ecological parameters. Because of the inherent frequency dependence of selection on reproductive traits in density-regulated populations (Maynard Smith 1982; Morgan *et al.* 1997), we carry out an evolutionary invasion analysis within the framework of adaptive dynamics theory (Metz *et al.* 1992, 1996; Dieckmann 1997). For simplicity, the evolution of selfing rates is modelled phenotypically, which is a classical approach in models of evolutionary game theory (Maynard Smith 1982). On this basis, we derive expressions for the outcome of selfing evolution governed by inbreeding depression and the cost of outcrossing. The evolution of selfing is first considered under stable population dynamics before we extend our analysis to non-equilibrium population dynamics and fluctuating environments. The main conclusions from this study are that both population dynamics and the nature of competitive interactions critically affect the evolution of selfing and are likely to give rise to evolutionarily stable intermediate selfing rates.

2. MODEL DESCRIPTION

In this section, we describe a general demographic model for an annual hermaphroditic organism. Self-fertilization occurs at a rate R, and each individual produces S ovules. In a monomorphic population and in the absence of selection, the growth ratio of the population is therefore given by the sum of SR inbred zygotes and $S(1-R)$ outbred zygotes.

(a) *Inbreeding depression and density regulation*

As a result of inbreeding depression, the organism's growth ratio can be lowered in two ways. First, we define a density independent and constant component of inbreeding depression, denoted by δ_0, which describes the decreased relative fitness of inbred individuals (Lloyd 1992). When the population density N_t at time t is close to zero, its dynamics can be described by

$$N_{t+1} = S[R(1-\delta_0) + (1-R)]\, N_t. \tag{2.1}$$

These dynamics do not yet incorporate density regulation. Second, based on Ricker's model (May & Oster 1976; Warner & Chesson 1985), we therefore consider the differential probabilities F_{in} and F_{out} for inbred and outbred individuals to survive density regulation,

$$F_{in} = \exp(-f_{in}\, N_t/K), \tag{2.2a}$$

$$F_{out} = \exp(-f_{out} N_t/K), \tag{2.2b}$$

where K is the population's carrying capacity. Because in each generation before density regulation the fractions of inbred and outbred individuals are given by the selfing rate R and by $1-R$, respectively, f_{in} and f_{out} are given by

$$f_{in}(R) = aR + c(1-R), \tag{2.3a}$$

$$f_{out}(R) = bR + d(1-R), \tag{2.3b}$$

where the competition coefficients a and b measure the competition effect exerted by inbred on inbred individuals and by inbred on outbred individuals, respectively. Similarly, c and d define the effect of outbred on inbred and of outbred on outbred individuals, respectively. The dynamics of the density-regulated population with selfing rate R is thus described by the following difference equation,

$$N_{t+1} = S\,[R(1-\delta_0)\exp(-f_{in}\, N_t/K) + (1-R)\exp(-f_{out} N_t/K)]\, N_t. \tag{2.4}$$

Given a population density N_t, the inbreeding depression δ can be determined. It is defined as 1 minus the relative fitness of selfed progeny (Charlesworth & Charlesworth 1987),

$$\delta = 1 - \frac{(1-\delta_0)\exp(-f_{in}\, N_t/K)}{\exp(-f_{out} N_t/K)}. \tag{2.5}$$

For the sake of simplicity, we choose the unit of population density such that $K=1$ for the evolution of selfing (except when fluctuating carrying capacities are considered).

(b) *Dynamical properties of the demographic model*

The equilibrium density N_{eq} is found by solving equation (2.4) for $N_{eq,t+1} = N_{eq,t}$. The non-trivial equilibrium $N_{eq} \neq 0$ can be obtained analytically for $R=0$,

$$N_{eq} = K \log(S)/d \tag{2.6a}$$

and for $R=1$,

$$N_{eq} = K \log(S(1-\delta_0))/a. \tag{2.6b}$$

For other selfing rates, equilibrium densities are determined numerically.

The non-trivial equilibrium may be dynamically stable or unstable. A full bifurcation analysis is not straightforward because of the number of parameters. However, for parameters a, b, c, d of the same order of magnitude (such as those used in this paper), the demographic behaviour is dominated by the fecundity S. The equilibrium is stable for low fecundity, whereas, analogously to Ricker's model (May & Oster 1976), cyclical and chaotic dynamics appear for higher fecundities. Figure 1 illustrates the dynamical behaviour for two particular sets of parameters.

(c) *Mutant growth rate and evolutionary invasion analysis*

Our approach utilizes the framework of adaptive dynamics theory, which is based on the concept of invasion fitness (Metz *et al.* 1992, 1996; Geritz *et al.* 1998). The ability of a mutant phenotype to invade a given resident population is evaluated by studying the growth ratio of the mutant when it is rare. As is customary in evolutionary ecology, we assume a separation of ecological and evolutionary time-scales (e.g. Doebeli & Dieckmann 2000) such that mutations are rare enough for mutants to appear in populations that have come close to their ecological equilibrium.

The fitness of an individual is measured as the number of gametes transmitted to the next generation (Uyenoyama *et al.* 1993) and is thus given by the sum of three components: selfed zygotes, outcrossed zygotes and zygotes of other individuals produced by fertilization with exported male gametes (Lloyd 1992). Selfed zygotes receive two gametes from their mother, whereas

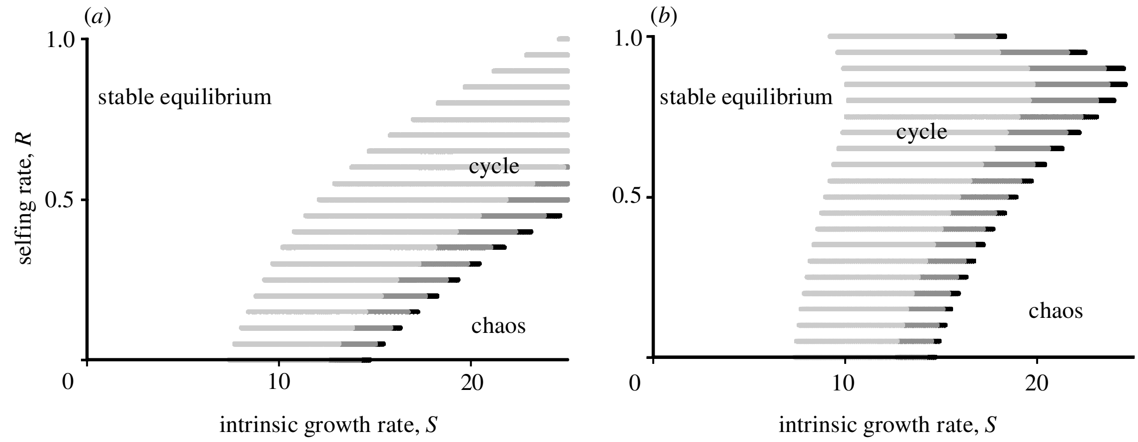

Figure 1. Bifurcation diagrams for the demographic model described by equation (2.4). From left to right: stable equilibria (white); cyclic dynamics with two, four and eight cycles or more (grey to black); and chaotic dynamics (white). Parameters: (*a*) $a = c = 1$, $b = d = 1.5$ and $\delta_0 = 0.7$; (*b*) $a = d = 1$, $b = 0.5$, $c = 1.3$ and $\delta_0 = 0.2$.

outcrossed zygotes receive only one. We assume that the number of male gametes used for self-fertilization is negligible. Thus the selfing rate does not influence the export of male gametes. As long as the mutant phenotype is rare, it competes virtually exclusively with resident phenotypes. Accordingly, the dynamics of a mutant phenotype with selfing rate R' in a resident population with selfing rate R is

$$N'_{t+1} = S[R'\ (1-\delta_0)\exp(-f_{\text{in}}\,N_{tr}/K) + \tfrac{1}{2}(1-R'+1-R)\exp(-f_{\text{out}}\,N_t/K)]N'_t, \qquad (2.7)$$

where N'_t is the density of mutants at time t. The ratio N'_{t+1}/N'_t defines the growth ratio of the mutant at time t, and thus the mutant's fitness in the resident's environment, $W(R',R)$ (Metz *et al.* 1992). Values of $W(R',R)$ larger than unity imply that the mutant can grow and invade the resident population, whereas values of $W(R',R)$ smaller than unity imply that the mutant dies out.

The fitness gradient $g(R)$ is given by the first derivative of W with respect to R' evaluated at R. A positive value of $g(R)$ means that, in the vicinity of R, mutants with $R' > R$ can invade the resident phenotype R, whereas a negative value of $g(R)$ means that mutants with $R' < R$ can invade (Geritz *et al.* 1997). Evolutionarily singular phenotypes R^* are defined as those that lead to a vanishing selection gradient, $g(R^*)$.

Two properties of singular phenotypes are regularly considered (Dieckmann 1997; Geritz *et al.* 1998). First, a singular phenotype R^* is convergence-stable or evolutionarily attainable (Eshel 1983; Christiansen 1991) if a resident population that is close to but not at R^* can be invaded by mutants that are closer to R^*. A convergence-stable singular phenotype (or convergence-stable strategy) is an evolutionary attractor in the sense that gradual evolution by small mutational steps will converge towards it, whereas a singular phenotype that is not convergence-stable acts as an evolutionary repellor. Second, a singular phenotype R^* is locally evolutionarily stable if no nearby mutant can invade the resident population at R^*. The properties of singular phenotypes are characterized either by analytical criteria or by the graphical evaluation of so-called pairwise invasibility plots (PIPs), in which the sign of $W - 1$ is depicted for every possible combination of mutant and resident phenotypes (Metz *et al.* 1996; Dieckmann 1997; Geritz *et al.* 1997, 1998). Examples of such plots are shown in figure 2.

3. EVOLUTION OF SELFING UNDER STABLE DEMOGRAPHIC CONDITIONS

(a) *The singular selfing rate and its stability*

For a non-trivial demographic equilibrium N_{eq}, the singular selfing rate R^* for which the selection gradient vanishes,

$$g(R^*) = \left.\frac{\partial W(R',R)}{\partial R'}\right|_{R'=R=R^*} = 0, \qquad (3.1)$$

is obtained as

$$R^* = \frac{\log(2(1-\delta_0))/N_{\text{eq}} - c + d}{(a+d)-(b+c)}, \qquad (3.2a)$$

provided that $(a+d)-(b+c) \neq 0$. As shown in Appendix A, solving equation (3.1) is equivalent to solving for $\delta = \frac{1}{2}$ with δ being a function of R^* and N_{eq}; this means that, at the singular selfing rate, the cost of outcrossing is exactly balanced by inbreeding depression. The equilibrium density N_{eq} at the singular selfing rate R^* is obtained from equation (2.4),

$$N_{\text{eq}} = \frac{\log(S\,(1-\frac{1}{2}R^*))}{bR^* + d(1-R^*)}, \qquad (3.2b)$$

(the detailed calculations are given in Appendix A). The singular selfing rate R^* and the corresponding equilibrium density N_{eq} are then obtained by solving equations (3.2*a*,*b*) numerically.

The singular selfing rate would be locally evolutionarily stable if R^* were a local maximum of the fitness function W,

$$\left.\frac{\partial^2 W(R',R)}{\partial^2 R'}\right|_{R'=R=R^*} < 0. \qquad (3.3a)$$

However, from the linearity of the fitness function in R', equation (2.7), we immediately see that, at the singular selfing rate, the fitness function's second derivative with respect to the mutant phenotype is zero, which means that

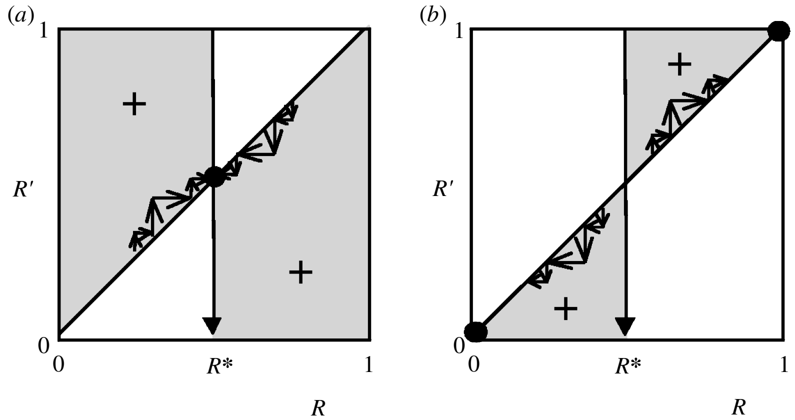

Figure 2. The two possible evolutionary outcomes of selfing evolution under stable demographic conditions. The resident selfing rate R varies along the horizontal axis and the mutant selfing rate R' along the vertical axis. Each of the two PIPs (Geritz *et al.* 1998) depicts the sign of $W(R',R) - 1$, where W is the mutant's invasion fitness (its time-averaged growth ratio) in the resident's environment. Grey areas indicate positive values: here, the mutant can invade. In the white areas, $W - 1$ is negative and the mutant cannot invade. On the main diagonal, $W - 1$ has to vanish because the resident phenotype is neutral in its own environment. At the singular selfing rate $R = R^*$, $W - 1$ also vanishes: under the linear model in equation (2.7) any mutant is neutral at R^*. The convergence stability of R^* is determined by the relative position of grey areas around R^*. (*a*) Here, R^* is convergence stable (an evolutionary attractor) because whatever is the initial resident population, any mutant closer to R^* will be selected for. The resulting phenotypic substitutions are shown as arrows, and R^* evidently represents the outcome of this evolutionary substitution process (black dot). (*b*) Here, R^* is not convergence stable (an evolutionary repellor) because the course of evolution leads away from R^*. The evolutionary outcomes of selfing evolution depend on the initial condition in R and are given by the lower and upper bounds of the selfing rate (black dots at $R = 0$ and $R = 1$, respectively).

all mutations are neutral at the singular selfing rate (Meszéna *et al.* 2000).

The singular selfing rate is convergence stable if, at R^*, the selection gradient g is a decreasing function of R (Geritz *et al.* 1998),

$$\left.\frac{\mathrm{d}g(R)}{\mathrm{d}R}\right|_{R=R^*} = \left[\frac{\partial^2 W(R',R)}{\partial R \partial R'} + \frac{\partial^2 W(R',R)}{\partial^2 R'}\right]\Bigg|_{R'=R=R^*} < 0. \tag{3.3b}$$

Since the second term in the square bracket vanishes due to the linearity of the fitness function, the convergence criterion reduces to

$$\left.\frac{\partial^2 W(R',R)}{\partial R \partial R'}\right|_{R'=R=R^*} = [-(a-c)+(b-d)]N_{\mathrm{eq}} - (f_{\mathrm{in}} - f_{\mathrm{out}})\left.\frac{\mathrm{d}N_{\mathrm{eq}}}{\mathrm{d}R}\right|_{R=R^*} < 0, \tag{3.4a}$$

with

$$\left.\frac{\mathrm{d}N_{\mathrm{eq}}}{\mathrm{d}R}\right|_{R=R^*} = \frac{[R^*\,(c-a) + 2(1-R^*)\,(d-b)]\,N_{\mathrm{eq}} - 1}{R^*\,f_{\mathrm{in}}(R^*) + 2(1-R^*)\,f_{\mathrm{out}}(R^*)}, \tag{3.4b}$$

(the detailed calculations are given in Appendix B). From these results we can conclude that only two types of configuration are possible for the PIPs describing the evolution of the selfing rate (see figure 2).

In the general demographic model investigated here, the competitive effects of inbred on inbred (competition coefficient a), inbred on outbred (b), outbred on inbred (c) and outbred on outbred (d) individuals are all allowed to be different. However, in the special case $a = c$ and $b = d$, competitive effects become independent of the frequency of inbred and outbred individuals (see equations (2.3)). We refer to this case—in which inbreeding depression is only affected by the total density of inbred and outbred individuals (see equation (2.5))—as the 'density-dependent model'. By contrast, the general case without any restrictions on the competition coefficients a, b, c and d—in which inbreeding depression is not only affected by population density but also by the relative frequencies of inbred and outbred individuals—is referred to as the 'frequency-dependent model'.

(b) *Evolution of selfing in the density-dependent model*

In the most trivial case in which inbred and outbred individuals are equally affected by density, $a = b = c = d$, the selection gradient never vanishes and depends only on δ_0. For $\delta_0 < \frac{1}{2}$ we have $g(R) > 0$ for all R and complete selfing at $R = 1$ will evolve, whereas for $\delta_0 > \frac{1}{2}$ we have $g(R) < 0$ for all R and complete outcrossing at $R = 0$ will evolve. These simple results directly correspond to the classical predictions (Lloyd 1979).

For the slightly more general density-dependent model, $a = c$ and $b = d$, equations (3.2) do not apply, because the denominator in (3.2*a*) vanishes. In this case, the singular selfing rate is instead determined from

$$R^* = 2\,[1 - \exp(b\,N_{\mathrm{eq}})/S], \tag{3.5a}$$

with

$$N_{\mathrm{eq}} = \frac{\log(2(1-\delta_0))}{a-b}. \tag{3.5b}$$

The condition for convergence stability of R^* in the density-dependent model is given by $a < b$ (see Appendix B). The biological interpretation of this result is straightforward. As can be seen from equation (2.5), the condition $a < b$ implies that inbreeding depression is a monotonically decreasing function of the density. Because at R^* the

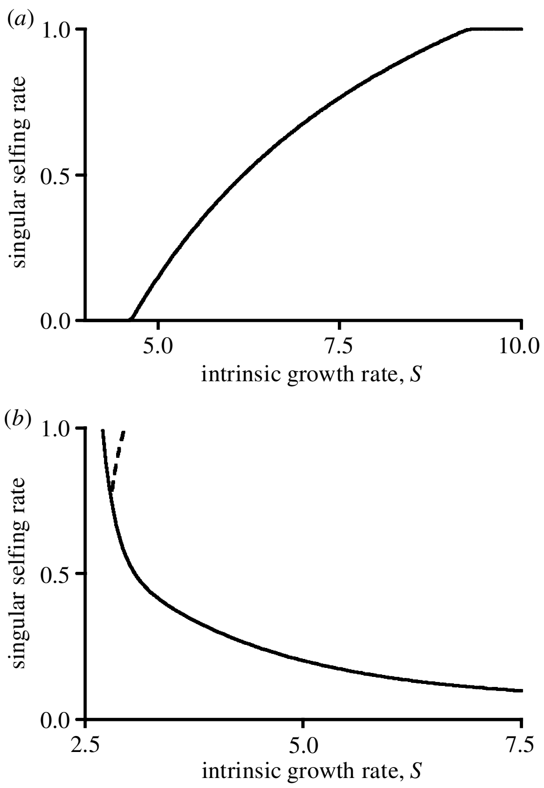

Figure 3. Evolution of selfing rates under stable demographic conditions as a function of fecundity S. (*a*) Density-dependent model. All depicted selfing rates are convergence stable. Parameters: $a = c = 1$, $b = d = 1.5$ and $\delta_0 = 0.7$. (*b*) Frequency-dependent model. For small S, two singular selfing rates are found, one is convergence stable (attractor, continuous line) and the other is not convergence stable (repellor, dashed line). Parameters: $a = 1$, $b = 0.6$, $c = 1.1$, $d = 1$ and $\delta_0 = 0.35$.

density N_{eq} decreases with the selfing rate (see equation (3.4*b*)) a further increase of selfing rates becomes increasingly difficult because of the simultaneous increase of inbreeding depression. This effect can stabilize intermediate selfing rates. An important conclusion from this is that, in the density-dependent model, a necessary condition for the evolution of intermediate selfing rates is that inbreeding depression decreases with population density. As $\delta = \frac{1}{2}$ at the singular selfing rate, this implies $\delta_0 > \frac{1}{2}$ as a necessary condition for evolution to result in intermediate selfing rates. Figure 3*a* illustrates how, in the density-dependent model, the resultant intermediate selfing rates increase with fecundity S.

(c) *Evolution of selfing in the frequency-dependent model*

We now consider the evolution of selfing in the general model, which allows for differential competitive interactions between all four combinations of inbred and outbred types. The singular selfing rate R^* is given by equations (3.2) and its convergence stability is determined by inequality (3.4*a*). The expression on the left-hand side of this inequality has two terms. The first term is directly determined by the four competition coefficients, whereas the second term depends on how the equilibrium density varies around the singular selfing rate. In most cases, the second term is small compared with the first one.

To facilitate understanding, let us explore the case $a = d$, which means that the competitive effects exerted by inbred on inbred individuals equal the effects exerted by outbred on outbred individuals. Let us also assume that the competitive effects exerted by outbred on inbred individuals are high ($c > a = d$), whereas those exerted by inbred on outbred individuals are low ($b < a = d$). In contrast to the density-dependent model, inbreeding depression is now an increasing function of density (see equation (2.5)). Under these conditions, stable intermediate selfing rates can be maintained. Figure 3*b* illustrates how, in the frequency-dependent model, the resultant intermediate selfing rates decrease with fecundity S.

In the general frequency-dependent model, we have thus identified an additional second mechanism that can lead to the evolutionary origin and maintenance of intermediate selfing rates. Contrary to the results for the merely density-dependent model, this phenomenon occurs even if inbreeding depression increases with density. If within-type competitive effects are equal for inbred and outbred types, $a = d$, the evolution and maintenance of intermediate selfing rates occurs if the competitive effect of inbred on outbred individuals, b, is sufficiently lower than the competitive effect of outbred on inbred individuals, c, with sufficiency being determined by the magnitude of the second term in inequality (equation (3.4*a*)). This means that the outbred individuals have to excel in the between-type competition with the inbred individuals. The between-type advantage of outbred individuals required for intermediate selfing rates can even be lower if they also have a direct within-type advantage, $a > d$, whereas it must be higher if the within-type advantage instead favours inbred individuals, $a < d$.

4. EVOLUTION OF SELFING IN FLUCTUATING POPULATIONS

In this section, we consider the outcome of selfing evolution by relaxing the assumption of stable population dynamical equilibria. Fluctuations in population density can arise because of the demographic properties of the model. Specifically, because generations are discrete, a high density in one generation induces high mortality and thus low density in the next generation: this can lead to deterministic cyclical or chaotic dynamics. Another option is stochastic fluctuations in the carrying capacity K; here, we explore a simple case of environmental fluctuations in which the carrying capacity in a given generation is given by K_1 with probability p and by K_2 with probability $1 - p$.

As the mutant growth ratio given by equation (2.7) is not constant over time when densities fluctuate, the fitness function $W(R',R)$ is determined numerically as the time-averaged growth ratio of the mutant population. This ratio is easily obtained by introducing a mutant at a very low frequency into the stationary resident environment and observing its dynamics, as described by equation (2.7), for a few hundred generations. Graphical illustration of the results in terms of PIPs is then straightforward.

Our aim here is to show that the convergence stability and evolutionary stability of singular selfing rates is crucially affected by fluctuating population densities, and that therefore the evolution of selfing can take a radically different course under such conditions. For greater clarity,

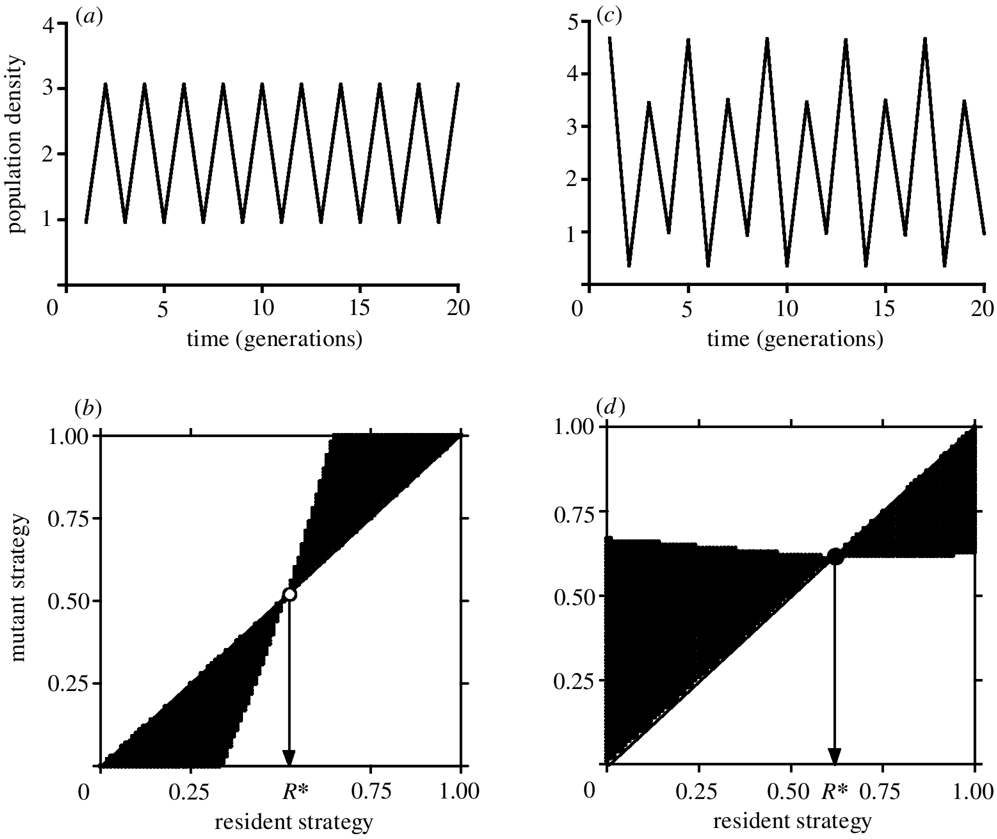

Figure 4. Evolution of selfing rates under deterministic density fluctuations. The panels at the top illustrate population density fluctuations at R^*, whereas the panels at the bottom show the corresponding PIPs. (*a*,*b*) Population densities exhibit a two cycle; the singular selfing rate is evolutionarily stable but not convergence stable. Parameters: $a = c = 1.3$, $b = d = 1$, $\delta_0 = 0.2$ and $S = 10$ (*c*,*d*) Population densities exhibit a four cycle; the singular selfing rate is both evolutionarily stable and convergence stable. Parameters: $a = c = 1.3$, $b = d = 1$, $\delta_0 = 0$ and $S = 15$.

we focus our analysis on the density-dependent model. This shows most clearly how density fluctuations can broaden the scope for the evolution of intermediate selfing rates, which otherwise is rather limited in the merely density-dependent model. For the same reason, we consider the case $a = c > b = d$, for which inbreeding depression increases with density. As we have shown above, this case does not allow for the evolutionary maintenance of intermediate selfing rates under stable demographic conditions.

(a) *Deterministic demographic fluctuations*

We choose the fecundity S to be sufficiently large for non-equilibrium population dynamics to ensue. Figure 4*a* illustrates the population dynamics for the case of two cycles. Figure 4*b* shows the resultant PIP. Comparing this plot with figure 2*a*,*b*, we see that the density fluctuations cause the singular selfing rate to become evolutionarily stable and inequality (equation (3.3*a*)) is now fulfilled: once the population has reached R^*, no mutant can invade. The singular selfing rate R^* is not convergence-stable because, in a resident population near R^*, a mutant closer to R^* cannot invade; inequality (equation (3.3*b*)) therefore is not fulfilled. This first example thus illustrates that the evolutionary stability of the singular selfing rate can be qualitatively affected by density fluctuations.

As a second example we consider a four-cycle population dynamic, figure 4*c*. Figure 4*d* shows the resultant PIP. We immediately see that the singular selfing rate now is evolutionarily stable as well as convergence stable. The second example thus illustrates that the convergence stability of the singular selfing rate can be qualitatively affected by density fluctuations.

(b) *Stochastic environmental fluctuations*

It is interesting to confirm whether the conclusions for deterministic density fluctuations also hold if such fluctuations are stochastic; a common mechanism for the latter is random variations in the carrying capacity of a population between generations (Mathias *et al.* 2001). We show here that the same qualitative results apply.

For this purpose, we choose a low value for the fecundity S that does not give rise to cyclical or chaotic dynamics. In the first example, we consider a small variance of the carrying capacity ($K_1 = 1$, $K_2 = 3$, and $p = \frac{1}{2}$). The resultant population dynamics are depicted in figure 5*a* and the corresponding PIP in figure 5*b*. In the second example, similar to the two-cycle dynamics, the singular selfing rate R^* becomes evolutionarily stable. A larger variance of the carrying capacity ($K_1 = 1$, $K_2 = 5$, and $p = \frac{1}{2}$) results in a convergence-stable singular selfing rate (figure 5*c*,*d*).

These two examples of stochastic density fluctuations reveal a very interesting property of evolution around the singular selfing rate R^*: the dependence of the two types of stability on the dynamics of the population. This allows us to identify a third mechanism for the evolutionary origin: the maintenance of intermediate selfing rates. Under

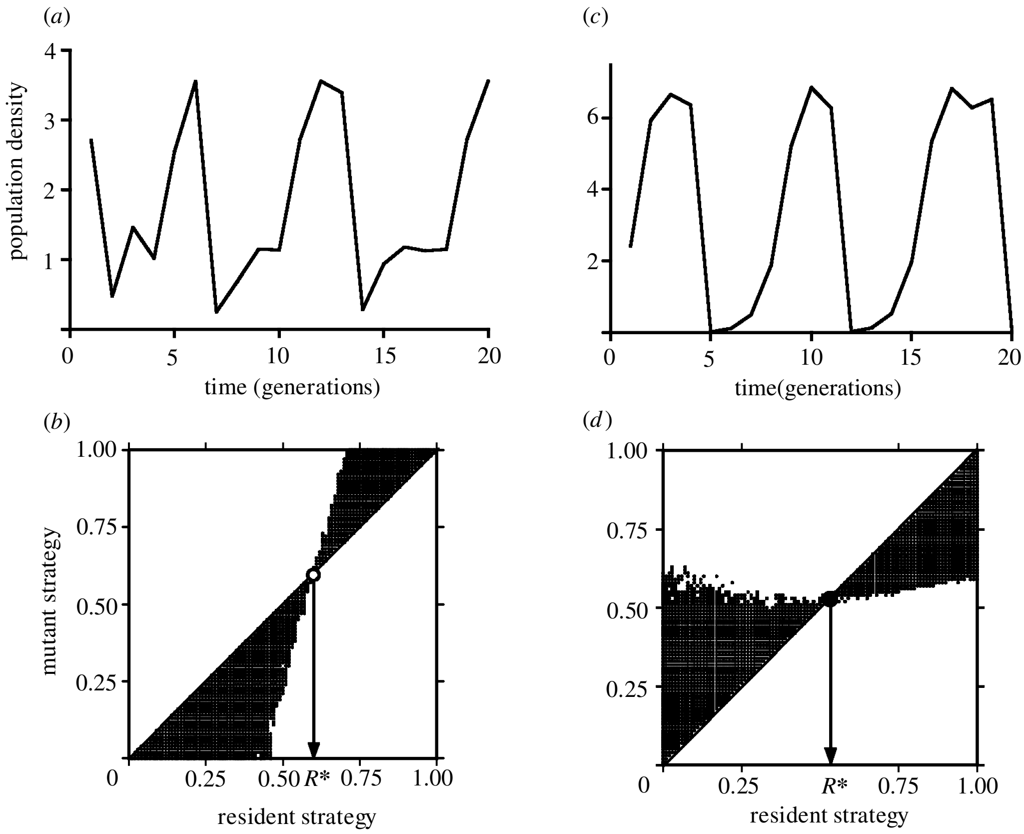

Figure 5. Evolution of selfing rates under stochastic density fluctuations. The panels at the top illustrate population density fluctuations at R^*, whereas the panels at the bottom show the corresponding PIPs. (*a*,*b*) The singular strategy is evolutionarily stable but not convergence stable. Parameters: $a = c = 1.3$, $b = d = 1$, $\delta_0 = 0.3$, $S = 4.5$, $K_1 = 1$, $K_2 = 3$ and $p = 0.5$. (*c*,*d*) The singular strategy is both evolutionarily stable and convergence stable. Parameters: $a = c = 1.3$, $b = d = 1$, $\delta_0 = 0.3$, $S = 5$, $K_1 = 1$, $K_2 = 5$ and $p = 0.5$.

stable demographic conditions, convergence-stable intermediate selfing rates require inbreeding depression to decrease with selfing rates, ($a = c < b = d$). When population densities fluctuate, this condition no longer applies and intermediate selfing rates evolve under a wider range of ecological conditions. Although we have shown only a few specific examples here, increasing the variance of density fluctuations generally facilitates the existence of convergence-stable intermediate selfing rates.

5. DISCUSSION

Based on the antagonistic selection pressures resulting from inbreeding depression and the cost of outcrossing, previous models have predicted that only complete selfing or full outcrossing are possible as outcomes of the evolution of selfing rates (Lloyd 1979). The same conclusion holds when inbreeding depression is caused by partially recessive deleterious mutations (partial dominance hypothesis (Charlesworth & Charlesworth 1987)), because inbreeding depression decreases with selfing rate (Charlesworth *et al.* 1990); the evolution of selfing then experiences a positive feedback. In general, the maintenance of partial selfing instead requires the gain in fitness to decrease with selfing rate, thus resulting in a negative feedback.

In this paper, we have shown that embedding studies on the evolution of selfing in population dynamical models of inbreeding depression can radically modify these conclusions, even though the evolution of selfing remains governed by inbreeding depression and the cost of outcrossing. Specifically, we have identified three types of negative feedback that all allow for the evolutionary origin and subsequent maintenance of intermediate selfing rates.

First, a negative feedback on selfing can arise when inbreeding depression decreases with density (as demonstrated by our merely density-dependent model). It is questionable whether this condition applies to many natural populations as it is generally assumed that stressful conditions (in this case, increasing density) lead to the increase of inbreeding depression (Wright 1977). Beyond this widely accepted rule of thumb, however, the general pattern is probably not that simple. An empirical study by Cheptou *et al.* (2001) could not identify any effect of density on inbreeding depression in the outcrossing plant *Crepis sancta*, whereas H. P. Koelewijn (unpublished results) has found that inbreeding depression in *Plantago coronopus* actually decreases with density, which, according to our analysis here, could create a negative feedback selecting for intermediate selfing rates.

Second, for the general frequency-dependent model analysed in this paper, we have identified another biological mechanism for creating the required negative feedback. Even when inbreeding depression increases with density, the evolutionary maintenance of intermediate selfing rates is expected if outbred individuals excel in competition with inbred individuals. No empirical data are yet available to confirm or refute that such a competitive asymmetry can occur. Our model suggests analysing the nature of competitive interactions within and between inbred and outbred types by estimating the corresponding competition coefficients directly from experimental studies.

Third, we have shown that fluctuations in population densities can induce a negative feedback on selfing. This result agrees with recent work by Cheptou & Mathias (2001) that has shown that stochastic inbreeding depression can maintain intermediate selfing rates (see also Cheptou & Schoen 2002). To a certain extent, our results can be considered as a particular case of fluctuating inbreeding depression caused by fluctuating population density. However, it is interesting to note that stochastic variations in carrying capacity generate the same type of negative feedback. In natural populations, variation in carrying capacities is a rather common phenomenon (Mathias *et al.* 2001) and can result from a wide range of natural causes, like variations in precipitation, temperature, nutrient inflow, prey abundance, or a species' exposure to predators or interspecific competitors.

This paper emphasizes that linking the fitness associated with particular selfing rates to the environmental conditions experienced by individuals expressing such rates modifies the evolution of selfing by influencing inbreeding depression. This implies that the dynamics of deleterious mutations causing inbreeding depression is not only affected by inbreeding itself (which has been studied in a supposedly constant selective environments by considering the genetic processes that purge deleterious mutations (Charlesworth *et al.* 1990)), but also by the ecological and environmental conditions experienced by individuals. Kondrashov & Houle (1994) distinguished types of mutation depending on the dependence of their expression on environmental conditions and showed that the estimation of mutation rates in *Drosophila* is affected by the environments in which these mutations originate. Recently, the process of purging of deleterious mutations has also been found to be less efficient under benign environmental conditions than in harsh environments (Bijlsma *et al.* 1999). Clearly, future theoretical work on these issues could benefit from combining the study of genetic effects with an ecologically explicit perspective on fitness as developed in this paper.

It should be noted that taking into account other ecological mechanisms beyond intraspecific competition, such as pollination mechanisms, can modify the transmission bias of selfing (changing in turn, the cost of outcrossing) and thus also allow for the maintenance of intermediate selfing rates (Holsinger 1996). The present paper has demonstrated that no such interspecific interactions need be considered for understanding qualitative departures from classical expectations regarding the evolution of selfing.

APPENDIX A: SINGULAR SELFING RATE AT THE STABLE DEMOGRAPHIC EQUILIBRIUM

Assuming a stable demographic equilibrium N_{eq}, the growth ratio of a mutant is given by equation (2.7),

$$W(R',R) = S\{R'(1-\delta_0)\exp(-[a\,R + c(1-R)]\,N_{eq}) + \tfrac{1}{2}(1-R+1-R')(1-R) \times \exp(-[b\,R + d\,(1-R)]\,N_{eq})\}. \quad \text{(A 1)}$$

The singular selfing rate is obtained from solving

$$\left.\frac{\partial W(R',R)}{\partial R'}\right|_{R'=R=R^*} = S\{(1-\delta_0) \times \exp(-[a\,R^* + c\,(1-R^*)]\,N_{eq}) - \tfrac{1}{2}\exp(-[b\,R^* + d\,(1-R^*)]\,N_{eq})\} = 0, \quad \text{(A 2)}$$

(it appears that equation (A 2) implies $\delta = 0.5$), which leads to the solution

$$R^* = \frac{\log(2(1-\delta_0))/N_{eq} - c + d}{(a+d)-(b+c)}, \quad \text{(A 3)}$$

for $(a+d)-(b+c) \neq 0$. At R^*, we obtain from equation (A 2)

$$(1-\delta_0)\exp(-[a\,R^* + c\,(1-R^*)]\,N_{eq}) = \tfrac{1}{2}\exp(-[b\,R^* + d\,(1-R^*)]\,N_{eq}). \quad \text{(A 4)}$$

Substituting equation (A 4) into equation (2.4) gives

$$S[\tfrac{1}{2}R + (1-R^*)]\exp(-[b\,R^* + d\,(1-R^*)]\,N_{eq}) = 1, \quad \text{(A 5)}$$

which allows us to determine N_{eq} at R^*,

$$N_{eq} = \frac{\log(S\,(1-\tfrac{1}{2}R^*))}{b\,R^* + d\,(1-R^*)}. \quad \text{(A 6)}$$

Solutions (N_{eq}, R^*) are found numerically by solving equations (A 3) and (A 6).

For $(a+d)-(b+c) = 0$, solving equation (A 2) yields

$$N_{eq} = \frac{\log(2\,(1-\delta_0))}{c-d} \quad \text{(A 7)}$$

and R^* is then obtained from substituting equation (A 7) into equation (A 6).

For the density-dependent model, $a = c$ and $b = d$, explicit solutions (N_{eq}, R^*) can be found,

$$R^* = 2[1 - \exp(b\,N_{eq})/S] \quad \text{(A 8)}$$

and

$$N_{eq} = \frac{\log(2\,(1-\delta_0))}{a-b}. \quad \text{(A 9)}$$

APPENDIX B: CONVERGENCE STABILITY AT THE STABLE DEMOGRAPHIC EQUILIBRIUM

Because of the linearity of equation (A 1) in R', the criterion for convergence stability reduces to

$$\left.\frac{\partial^2 W(R',R)}{\partial R\,\partial R'}\right|_{R'=R=R^*} < 0. \quad \text{(B 1)}$$

From equation (A 2) one obtains

$$\left.\frac{\partial^2 W(R',R)}{\partial R \partial R'}\right|_{R'=R=R^*} = (1-\delta_0)\left\{-(a-c)\,N_{eq} + [a\,R^* + c\,(1-R^*)]\left.\frac{dN_{eq}}{dR}\right|_{R=R^*}\right\} \times \exp(-[a\,R^* + c\,(1-R^*)]\,N_{eq}) - \tfrac{1}{2}\left\{-(b-d)\,N_{eq} + [b\,R^* + d\,(1-R^*)]\left.\frac{dN_{eq}}{dR}\right|_{R=R^*}\right\} \times \exp(-[b\,R^* + d\,(1-R^*)]\,N_{eq}). \quad \text{(B 2)}$$

At R^*, equation (A 4) can be used to show that condition (B 2) is equivalent to

$$[-(a-c) + (b-d)]\,N_{eq} - (f_{in} - f_{out})\left.\frac{dN_{eq}}{dR}\right|_{R=R^*} < 0. \quad \text{(B 3)}$$

The first derivative in this expression is obtained by differentiating equation (2.4) with respect to R and evaluating the result at (N_{eq}, R^*), which gives

$$G = S\,\{R\,(1-\delta_0)\exp(-[a\,R + c\,(1-R)]\,N_{eq}) + (1-R)\exp(-[b\,R + d\,(1-R)]\,N_{eq}\} = 1. \quad \text{(B 4)}$$

Differentiating the implicit function G,

$$dG = \frac{\partial G}{\partial N_{eq}} dN_{eq} + \frac{\partial G}{\partial R} dR = 0, \quad \text{(B 5)}$$

gives

$$\frac{dN_{eq}}{dR} = -\frac{\partial G/\partial R}{\partial G/\partial N_{eq}}. \quad \text{(B 6)}$$

This yields

$$\left.\frac{dN_{eq}}{dR}\right|_{R=R^*} = \frac{[R^*\,(c-a) + 2(1-R^*)\,(d-b)]N_{eq} - 1}{R^* f_{in}(R^*) + 2(1-R^*)\,f_{out}(R^*)}. \quad \text{(B 7)}$$

In the density-dependent model, $a = c$ and $b = d$, the criterion for convergence stability reduces to

$$-\,(f_{in} - f_{out})\left.\frac{dN_{eq}}{dR}\right|_{R=R^*} < 0. \quad \text{(B 8)}$$

It can easily be shown that the derivative in this expression is negative. As $f_{in} = a = c$ and $f_{out} = b = d$, convergence stability in the density-dependent model applies if $a < b$.

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