



## A Lotka–Volterra Model of Coexistence between a Sexual Population and Multiple Asexual Clones

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(Received on 16 July 2001, Accepted in revised form on 25 February 2002)

At carrying capacity, small advantages in competitive ability can compensate a sexual population for its two-fold disadvantage in growth capacity when facing invasion by asexual mutants. In this paper, we develop a generic analytical model to consider the ecology of a sexual population comprising equal numbers of males and females, competing for shared prey resources with multiple female-only clones. We assume that the clones arise from the sexual population and are distinguished from it only by having narrower resource niches and twice the growth capacity. For sexual populations, at density-dependent carrying capacity, intra-specific competition between clonal individuals prevents them from realizing their two-fold advantage in intrinsic growth. This prediction leads to three novel outcomes: (i) a sexual population can coexist with any number of clones, provided their combined competitive impact remains less than the impact of the clones on each other; (ii) a sexual species can immediately exclude asexual invaders if it is a fast growing and strong competitor of shared resources and also has refuge in an abundant alternative resource; (iii) the rate of accumulation of clones in a sexual population will be slowed by intra and inter-specific competition amongst the clones themselves, in addition to the competitive impact from the original sexual population.

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### Introduction

Evolutionary biologists have long questioned how sex can persist in the face of competition from asexual modes of reproduction (Williams, 1975; Maynard Smith, 1978). The cost of sex is expressed in the potential for a sexual population to be invaded by individuals with asexual capacity arising from the sexual population. With no males to sustain, but being otherwise identical, the asexual genotype can double its

representation in the population of each generation. Asexual lines do arise within sexual species, even in some vertebrates (e.g. lizards: Ineich, 1999; fish: Vrijenhoek & Pfeiler, 1997). Since the prevailing mode of reproduction in nature is observed to be sexual, its two-fold cost is frequently used as a measure of the amount by which sex must benefit from the evolutionary advantages associated with its greater genetic variation (Hamilton *et al.*, 1990; Kondrashov, 1993; Hurst & Peck, 1996). To make such an equivalence, however, ignores a general principle of population ecology, that competing species can coexist by trading differences in growth

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capacity against differences in competitive ability (e.g. Nee & May, 1992; Nee *et al.*, 1997).

Recent work has shown how classical Lotka–Volterra dynamics can be used to quantify the ecological thresholds for coexistence of sexual populations with asexual mutant invaders (Doncaster *et al.*, 2000; Kerszberg, 2000). By partitioning net growth of consumers into separate rates of birth and death, the standard Lotka–Volterra competition equations are extended to encompass the trade-off between competition and growth that can ensure persistence of the sexual population. Small advantages in competitive ability can be enough to fully compensate a sexual population for its two-fold disadvantage in growth capacity. This competitive advantage can be small because the asexual individuals are competing amongst themselves for common resources, as well as competing to survive against the sexual individuals.

Previous ecological explanations for the prevalence of sex have been based on sib competition (Ghiselin, 1974; Bell, 1982; Burt & Bell, 1987) or complex simulations of character displacement induced by environmental influences on genetic structure (Case & Taper, 1986). In the sense that competition within a species can be regarded loosely as a form of sib-competition, analyses of Lotka–Volterra dynamics (Doncaster *et al.*, 2000; Kerzberg, 2000) and character displacement (Case & Taper, 1986) represent conceptually simple quantifications of the verbal arguments presented by Bell's (1982) "tangled bank" hypothesis. Neither of these analyses, however, distinguish sib-competition from other forms of intra-specific competition.

Models of sib-competition consider the influence of genetic variation on the intensity of competition amongst sexual siblings, compared to competition between self-identical asexual siblings (Williams & Mitton, 1973; Maynard Smith, 1976; Young, 1981). Advantages of sex are then inferred from differences in the resulting population growth rates for the two reproductive modes. It has been noted by Maynard Smith (1989, pp. 244–245) that sibling competition is not required for ecological models to counter balance the cost of males in the short term. Genetic variation has two distinctly different ecological consequences: reducing intra-specific

competition (sib-models) and reducing inter-specific competition (Lotka–Volterra and character displacement models), which may co-occur but are not necessarily found together. The numerous negative findings against sib-competition (Schmitt & Ehrhardt, 1987; Willson *et al.*, 1987; Kelley, 1989; Cheplick, 1992; Garcia & Toro, 1992) leave untested models of inter-specific competition. Since the models of inter-specific competition predict coexistence from differences in niche usage, they are close in concept to Vrijenhoek's (1979) "frozen niche variation hypothesis": that asexual lineages arise in a sexual population with genotypes frozen to those of the progenitor parent.

The purpose of this paper is to develop theory of inter-specific competition to encompass analytical models of resource competition between a sexual population and multiple asexual clones. Multiple clones are understood to be problematic for all theories for the maintenance of sexual reproduction that rely upon genetic diversity within the sexual population ("Red Queen": Lively & Howard, 1994; "frozen niche variation": West & Peters, 2000). This is because clonal diversity can confer on an asexual population the same benefits of genetic variation that are provided by sexual reproduction. For example, whereas each clone may exploit a relatively narrow niche, a diversity of different clones can, between them, encompass the complete resource niche of the sexual population (West & Peters, 2000).

The expanded Lotka–Volterra model presented here allows the conditions for coexistence between multiple clones and the progenitor sexual population to be calculated within the context of measurable ecological parameters. This is an analytical extension of the simulations of Weeks (1993), which investigated the consequences of repeated asexual invasions for the survival of a sexual population. His simulations were based on a model of soft truncation selection for clonal phenotypes with non-overlapping generations competing over a range of niches with a recombining sexual progenitor. Each clonal phenotype was present in proportion to its production of offspring, and there was no competition between clonal phenotypes. The Lotka–Volterra model, in contrast, only

accounts for recombination implicitly through an assumed relationship of genetic diversity to niche width. However, it achieves a higher level of ecological realism by modelling overlapping generations with density-dependent growth, in which offspring survive in proportion to the availability of continuously renewing resources. Different clonal types compete amongst each other for shared resource stocks as well as with the sexual progenitor population.

No previous models for coexistence in clonal assemblages have used the ecologically realistic framework of competition both between and within phenotypes competing for renewing resources to develop the generic conditions for coexistence. By doing so, we are able to experiment with the amount of niche overlap between multiple competing populations that will just sustain coexistence. The Lotka–Volterra structure uniquely allows us to express the ecological benefits of competitive advantage relative to slower growth capacity (Doncaster *et al.*, 2000; Kerszberg, 2000). We consider the particular case of competitive advantages to the sexual population brought about specifically by its having access to a wider resource base than any one clone. This is a realistic possibility if resource use is defined by genotype, given that the asexual invaders are genotypically self-identical (barring further mutations). The analysis assumes a relationship of genetic diversity to niche breadth in order to answer the following question: how much niche overlap can a sexual population sustain from clonal invaders?

Our first objective is to explore the conditions for competitive coexistence in the following version of the classical Lotka–Volterra rate equations:

$$\begin{aligned} \dot{N}_1 &= r_1 \left( 1 - \frac{N_1 + \alpha_{12}N_2}{K_1} \right) N_1 - d_1 N_1, \\ \dot{N}_2 &= r_2 \left( 1 - \frac{N_2 + \alpha_{21}N_1}{K_2} \right) N_2 - d_2 N_2. \end{aligned} \quad (1)$$

Parameters  $r_i$  and  $d_i$  are constants of proportionality for growth and death, respectively. The two competition coefficients,  $\alpha_{ij}$ , measure the impact *per capita* by species  $j$  on the growth of

species  $i$ , relative to the impact of  $i$  on its own growth to carrying capacity,  $K_i$ , where  $K_i$  is the carrying capacity of species  $i$  in the absence of death,  $d_i$ . Setting both eqns (1) to zero yields equilibrium solutions  $N_1^*$ ,  $N_2^*$ . The conditions for invasion by each species are then:

$$\begin{aligned} N_1^* > 0 \text{ if } : \alpha_{12}K_2 \left( 1 - \frac{d_2}{r_2} \right) < K_1 \left( 1 - \frac{d_1}{r_1} \right), \\ N_2^* > 0 \text{ if } : \alpha_{21}K_1 \left( 1 - \frac{d_1}{r_1} \right) < K_2 \left( 1 - \frac{d_2}{r_2} \right). \end{aligned} \quad (2)$$

In the original development of this model by Doncaster *et al.* (2000), the two predators competed for a single prey resource, allowing both  $K_i$  to be scaled to unity. This made it possible to define the two-fold growth advantage of an asexual mutant species 2 invading a sexual population of species 1 as simply  $r_2 = 2r_1$  (assuming  $d_1 = d_2$ ) and it gave the most stringent test for coexistence. Here, we define additional prey resources to which only the sexual population has access, giving it a wider resource niche than the asexual population and resulting in  $K_1 \neq K_2$  under most circumstances. Clearly from eqn (2), an asexual invasion may be prevented if  $K_1 \gg K_2$ . We will show, however, that niche breadth has a complicated relation to  $K_i$ , and that differences in niche breadth also result in  $r_2 \neq 2r_1$ , as well as changing the value of  $\alpha_{12}$  (though not of  $\alpha_{21}$ ). A surprising outcome is that the advantage to the sexual species of a broader feeding niche can be greater for small increases in breadth than large increases. We demonstrate this deterministically and test the robustness of our predictions with stochastic simulation. We then go on to explore cases of simultaneous invasion by two or more clones.

### Analytical Model

We extend the standard Lotka–Volterra predator–prey equations to the case of more than one predator species competing for a variety of prey species. Each predator species  $i$  has abundance  $N_i$  and grows in proportion to prey consumption. Each prey species  $j$  has abundance  $S_j$ , and grows logistically to its carrying capacity  $k_j$  in the absence of predation, from an intrinsic rate  $a_j$ . For simplicity we will

set  $k_j$  for all prey species to the same value. We will measure differences between the niche breadths of the predators in terms of their consumption rates of the prey species. The outcomes differ little from those obtained by setting all consumption rates to the same value and obtaining niche breadths from different  $k_j$ .

Assume each predator  $i$  consumes each prey  $j$  in proportion to its abundance, with a constant of proportionality  $c_{ij}$  for the *per capita* rate. Assume the birth rate *per capita* of predator  $i$  is proportional to its total consumption, with constant of proportionality  $b_i$ , and that population growth is offset by a constant death rate *per capita*  $d_i$ . The dynamics are represented by predator and prey rate equations:

$$\begin{aligned}\dot{N}_i &= b_i N_i [\mathbf{CS}]_i - d_i N_i, \\ \dot{S}_j &= a_j \left(1 - \frac{S_j}{k_j}\right) S_j - S_j [\mathbf{C}^T \mathbf{N}]_j,\end{aligned}\quad (3)$$

where  $\mathbf{C}$  is a 'consumption matrix' with entries  $c_{ij}$ , and  $\mathbf{N}$  and  $\mathbf{S}$  are column vectors with entries  $N_i$  and  $S_j$ , respectively. The total prey consumed *per capita* by predator  $i$  is the  $i$ -th element of the vector  $[\mathbf{CS}]$ . These equations represent the element-by-element dynamics of  $N_i$  and  $S_j$ .

### Predictions of the Analytical Model

We use eqn (3) to describe the dynamics of a sexual predator population  $N_1$  competing for a number of prey species with one or more asexual clones. As in previous papers (Doncaster *et al.*, 2000) we confer a two-fold cost of males on the sexual population by halving the rate at which it converts consumed prey into offspring,  $b_1$ , with respect to  $b_i$  of the other (asexual) species. This means that we assume an identical intrinsic birth rate for sexual females and asexual individuals, and zero birth rate for males which constitute half of the sexual population.

The niche width of a predator is defined by the range of prey species that it exploits. We assume that niche width reflects genetic variability, and we explore the realistic scenario of each clone having a sample of the genetic variation contained within the original sexual population (Vrijenhoek, 1979). This is represented in our

model by each clone exploiting a subset of the prey species available to the sexual population. In this sense, the clones have a narrower resource niche than the sexual population. To create a stringent test for the sexual population, we assume that all predator species have the same total rate of prey consumption *per capita*. This means that each row of the consumption matrix  $\mathbf{C}$  sums to the same value,  $c_{tot}$ .

We now examine cases that represent the range of scenarios possible under this model for a sexual population invaded by asexual clones. We start with the simplest case of a single invading clone, and incrementally add dimensions of niche space in further cases.

#### SEXUAL PREDATOR COMPETING WITH ONE CLONE AND RETAINING A RESOURCE REFUGE

The following consumption matrix describes a sexual population  $N_1$  competing with a single clone  $N_2$  that occupies a narrower resource niche:

$$\mathbf{C} = \begin{pmatrix} c_{11} & c_{12} \\ 0 & c_{22} \end{pmatrix}. \quad (4)$$

The rows of the matrix correspond to the consumption rates by each predator species of the available prey species (columns). The clone has a narrower feeding niche than the sexual, expressed in its consumption from  $S_2$  only, leaving  $S_1$  as a resource refuge for the sexual population. Since the total consumption rates of the two predators are equal,  $c_{11} + c_{12} = c_{22} = c_{tot}$ . Applying the consumption matrix in eqn (4) to the prey eqns (3) yields the expansion:

$$\begin{aligned}\dot{S}_1 &= a_1 \left(1 - \frac{S_1}{k_1}\right) S_1 - S_1 c_{11} N_1, \\ \dot{S}_2 &= a_2 \left(1 - \frac{S_2}{k_2}\right) S_2 - S_2 (c_{12} N_1 + c_{22} N_2).\end{aligned}\quad (5)$$

The predator dynamics given in eqns (3) expand to give

$$\begin{aligned}\dot{N}_1 &= b_1 N_1 (c_{11} S_1 + c_{12} S_2) - d_1 N_1, \\ \dot{N}_2 &= b_2 N_2 c_{22} S_2 - d_2 N_2.\end{aligned}\quad (6)$$

The prey eqns (5) can be solved for zero rates, and the equilibrium  $S_j$  inserted into the predator eqns (6) to obtain predator rates equivalent to the generic Lotka–Volterra eqns (1) (Appendix A). Table 1 shows the conversion to predator carrying capacity,  $K_i$ , intrinsic rate of growth,  $r_i$ , and competition coefficients,  $\alpha_{ij}$ .

We can now vary the size of  $c_{11}$  in order to find the size of refuge required by the sexual predator for it to persist in the event of an asexual invasion. Figure 1 shows that the consumption of prey 1 by the sexual predator 1 need not be large for it to withstand invasion from the clone. Indeed for a sexual predator with a high growth capacity, given by high  $r_1/d_1$  in eqn (1), the sexual population can drive the asexual extinct as  $c_{11}$  increases above small values [Fig. 1(b)]. This is because of its larger carrying capacity ( $K_1$  in Table 1) given by the exclusive access to prey 1. However, as  $c_{11}$  approaches  $c_{tot}$ , sex and asex coexist again as their niches diverge completely and the competition coefficients tend to zero ( $\alpha_{ij}$ , Table 1).

Other parameters that influence the outcome of the clonal invasion are the carrying capacities of the prey  $k_j$ . If all  $k_j$  are equal, larger values increase the advantage to  $N_1$  in similar fashion to higher growth capacities. Otherwise the prey species with the largest carrying capacities will

advantage those predators that exploit them in similar fashion to the advantage conferred by a higher consumption rate.

#### SIMULATION

A simulation of competing predators shows how niche overlap and growth capacity combine to influence the relative competitiveness of sexual and asexual populations. The simulation monitors a 1-D space of  $k$  cells over sequential time steps. Each cell can support one individual of each of two prey species. At each time step, each prey has probability  $a_j$  of producing a single new offspring, and all prey are redistributed at random between the  $k$  cells. These prey are consumed by a sexual predator with population  $N_1$ , and an asexual predator with population  $N_2$ . At each time step each predator has a probability  $d_i$  of dying. If it lives, an individual is randomly assigned a unique cell from which to sample prey. If prey are present within its cell, a predator 1 has probability  $c_{11}$  of consuming an individual of prey 1, and probability  $c_{12}$  of consuming an individual of prey 2. A predator 2 cannot consume prey 1, but consumes prey 2 with probability  $c_{22}$ . The consumption of a prey item gives each predator  $i$  a probability  $b_i$  of producing a single new offspring. The value of  $b_1$

TABLE 1  
*Definition of terms in eqn (1) for the general model of two predators with unequal niche breadths\**

Species	Term in eqn (1)	General model for two predators, two prey, $c_{21} = 0$
Predator 1	$r_1$	$b_1(c_{11}k_1 + c_{12}k_2)$
	$K_1$	$\frac{c_{11}k_1 + c_{12}k_2}{c_{11}^2k_1/a_1 + c_{12}^2k_2/a_2}$
	$\alpha_{12}$	$\frac{c_{12}c_{22}k_2/a_2}{c_{11}^2k_1/a_1 + c_{12}^2k_2/a_2}$
Predator 2	$r_2$	$b_2c_{22}k_2$
	$K_2$	$\frac{a_2}{c_{22}}$
	$\alpha_{21}$	$\frac{c_{12}}{c_{22}}$

\*Expansion of eqns (3)–(4) at prey equilibrium yields predator rates with identical dynamics to eqn (1) (Appendix A), as indicated by the equivalences in the table.

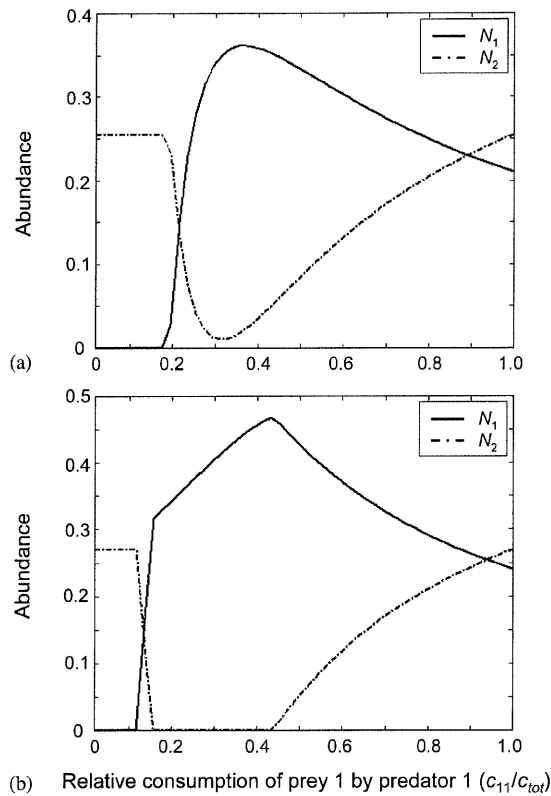


FIG. 1. Influence of niche breadth on coexistence for the consumption matrix shown in eqn (4). Equilibrium abundances of sexual predator 1 ( $N_1^*$ ) and asexual predator 2 ( $N_2^*$ ) are obtained by setting rate eqns (3) to zero (Appendix A). The graph shows their responses to relatively higher investment by the sexual population in prey 1 from left to right on the abscissa, given the condition that  $c_{11} + c_{12} = c_{22} = c_{tot}$ . (a) Relatively low population growth capacity of sexual predator 1, given by  $b_1(c_{11}k_1 + c_{12}k_2)/d_1$  [equivalent to  $r_1/d_1$  in eqn (1)]. The sexual and asexual populations coexist above a threshold value of  $c_{11}$ . Parameter values:  $a_1, a_2 = 0.15$ ,  $k_1, k_2 = 1$ ,  $b_1 = 0.1$ ,  $b_2 = 0.2$ ,  $d_1, d_2 = 0.015$ , and  $c_{tot} = 0.5$ . (b) Higher growth capacity of both predators given by  $d_1, d_2 = 0.01$ , other parameter values as for (a). The asexual population is driven to equilibrium extinction at larger values of  $c_{11}$ , representing a larger  $K_1$  while  $\alpha_{21}$  remains high [eqn (1) and Table 1].

is set to half that of  $b_2$ , since half the population of predator 1 is assumed to be comprised of males which do not themselves produce offspring.

Outcomes of the simulation for a range of niche breadths and growth capacities show sex winning in regions of parameter space where it competes with asex whilst retaining a resource refuge (Fig. 2). The slightly wider range of values of  $c_{11}$  over which sex wins, compared to the

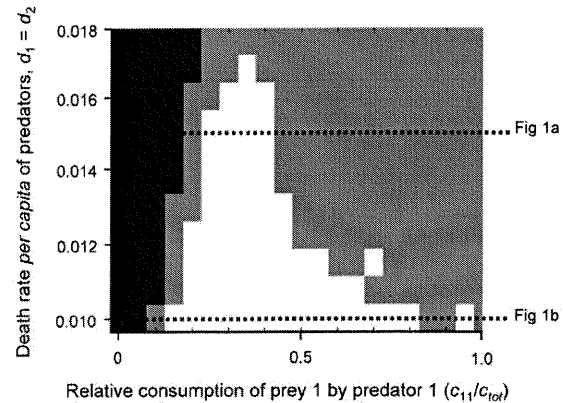


FIG. 2. Influence of niche breadth on coexistence for stochastic simulation of a sexual predator 1 competing with an asexual predator 2 for two prey species, where  $c_{11} + c_{12} = c_{22} = c_{tot}$ . Population abundances for each cell in the plots are averaged from 21 runs, each of 100 prey generations following an equilibration time of 2400 generations. Initial values:  $N_1, N_2 = 50$ ;  $S_1, S_2 = 1000$ . Graph shows increasing relative investment in prey 1 by predator 1 from left to right on the x-axis, and increasing death rate of both predators on the y-axis, expressing decreasing growth capacity from bottom to top. Shading distinguishes regions of parameter space where for the majority of runs asex wins: in black, where sex wins: in white, and where both coexist: in grey. Other parameter values for this simulation:  $a_1, a_2 = 0.15$ ;  $k_1, k_2 = 1000$ ;  $b_1 = 0.1$ ;  $b_2 = 0.2$ ;  $c_{22} = 0.5/k_j$ .

analytic outputs of Fig. 1, is attributable to stochastic effects on coexistence at small  $N_2$ .

#### SEXUAL PREDATOR COMPETING WITH TWO CLONES AND WITHOUT ANY FEEDING REFUGE

The potential for coexistence is greatly reduced by the introduction of a second clone that exploits the sexual predator's refuge from the first clone. The consumption matrix is

$$\mathbf{C} = \begin{pmatrix} c_{11} & c_{12} \\ 0 & c_{22} \\ c_{31} & 0 \end{pmatrix}. \quad (7)$$

Sex cannot coexist with asex in this case, unless we relax the condition that the rows of eqn (7) all sum to the same  $c_{tot}$ . The sexual population can then survive if  $c_{22} + c_{31} < c_{11} + c_{12}$  such that one of the clones has a sufficiently low total consumption rate for it to be extinguished by the sexual. It should be noted, however, that clones arising independently by

mutation from the sexual population may compete sequentially rather than simultaneously. The sexual population may repeatedly drive out a single clone [Figs 1(b) and 2], in which case the model reverts to the simpler case described in the previous section.

#### SEXUAL PREDATOR COMPETING WITH TWO CLONES

Coexistence with multiple clones necessitates a refuge for the sexual predator, which may take the form of a prey species that is under-exploited by the clones. We consider the general case of a sexual predator with a feeding niche of three prey, and two clones each of which is more or less specialist on one prey type. The consumption matrix then has no zero entries:

$$C = \begin{pmatrix} c_{11} & c_{12} & c_{13} \\ c_{21} & c_{22} & c_{23} \\ c_{31} & c_{32} & c_{33} \end{pmatrix}. \quad (8)$$

We use the simplex shown in Fig. 3 to explore the full range of possible competitive outcomes between the three predator populations under the condition that all have the same unitary rate of total prey consumption:  $c_{i1} + c_{i2} + c_{i3} = c_{tot}$  for  $i = 1, 2, 3$ . We start with a sexual predator 1 exploiting all three prey species equally. We then examine the effects of competition with the two asexual clones by plotting the outcome of every possible strategy by asexual predator 3 for a given strategy by asexual predator 2. Figure 4(a) and (b) shows two canonical cases for predator 2. They distinguish regions of parameter space in which sex coexists with one or both invading clones (coloured grey, green and dark blue) from those in which it is driven extinct (red and yellow).

The sexual population persists provided two conditions are met: (1) both clones have relatively narrow resource niches, meaning they are situated towards the edge of the simplex and therefore feeding primarily on one or two prey species; (2) at least one prey species is under-exploited by the clones and can act as a refuge for the sexual predator. The sexual population is invariably driven extinct by clones with consumption strategies lying on opposite sides

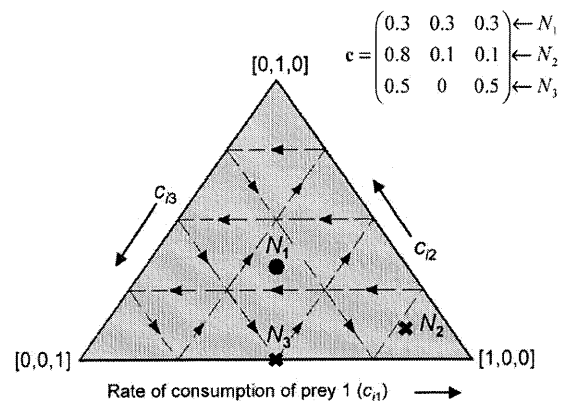


FIG. 3. Simplex for the full range of consumption strategies of three prey types that can be adopted by three predator populations under the condition  $c_{i1} + c_{i2} + c_{i3} = 1$ . The three axes represent the rates of consumption of each prey species. In this example the position of sexual predator population  $N_1$  (dot) indicates consumption of all of three prey types at equal rates. In contrast, the clonal population  $N_2$  consumes  $S_1$  preferentially, and the clonal population  $N_3$  consumes  $S_1$  and  $S_3$  equally and none of  $S_2$ .

of the simplex, as this removes any refuge for the sexual population.

Figure 4(a) and (b) show that any one clone can drive the other clone to extinction by being situated closer to the centre of the simplex. Likewise, there exist regions of simplex space in which the persistence of sex is unchanged by the addition of a second clone. The sexual population is unable to drive both clones to extinction in Fig. 4(a) and (b) because it makes intermediate use of all three prey types. If its niche lies closer to the edge of the simplex, then it too can be responsible for eradicating clones [in accordance with Figs 1(b) and 2]. If the sexual population has a faster growth capacity, this narrows the sector of the simplex in which it cannot coexist with competing clones (also in accordance with Figs 1 and 2).

#### SEXUAL PREDATOR COMPETING WITH THREE CLONES

The importance of a resource refuge for the sexual population is confirmed by extending the analysis to the case of a sexual population with a resource niche comprising four prey types. The sexual population can coexist with a number of clones provided at least one prey type is under-exploited by the asexual populations. This is

shown in Fig. 5 for a sexual population competing with three clonal species, where the consumption strategies of  $N_1$ ,  $N_2$  and  $N_3$  are fixed [eqn (9)] and the outcome of competition is evaluated for a range of consumption strategies of  $N_4$ .

$$C = \begin{pmatrix} 0.25 & 0.25 & 0.25 & 0.25 \\ 0.7 & 0.1 & 0.1 & 0.1 \\ 0.1 & 0.7 & 0.1 & 0.1 \\ c_{41} & c_{42} & c_{43} & c_{44} \end{pmatrix}. \quad (9)$$

The third clone may drive the sexual population to extinction if it has a broad consumption strategy, similar to that of the sexual population, or if the asexual populations between them efficiently exploit all four prey types. Otherwise the sexual population persists with all clones, or some coexisting clones may prevent establishment of others. The general conclusion is that if the sexual population can survive invasion by one clone, its persistence will not be affected by invasions of an additional clone provided it retains at least a small resource refuge. This applies equally to several additional clones as to one. Each additional clone adds an extra dimension to the analysis, however, making presentation difficult beyond four species. In reality, a large sexual population is likely to have a very much greater genetic variation than any one clone, represented by it occupying many more dimensions of niche breadth (e.g. Innes & Hebert, 1988). A great diversity of clones is then required to prevent the sexual population from retaining a resource refuge.

### Discussion

The analysis of the dynamics of resource competition shows how a sexual population can neutralize the competitive disadvantage of its lower growth capacity by having access to a wider resource base than its asexual competitor. It can retain this greater width if the combined competitive impact of multiple clones remains less than the competitive impact of the clones on each other. This is the same prediction as for a single clone, where coexistence is possible if inter-specific competitive impacts are less intense than intra-specific impacts (Doncaster *et al.*,

2000). In both cases, relatively small differences in parameters of ecological interaction lead to large differences in population growth rates, which can counterbalance the two-fold intrinsic advantage of asexual reproduction. This amplification occurs as a direct consequence of populations being held at density dependent carrying capacity by intra-specific competition, which prevents them from realizing their intrinsic growth capacities.

Our analysis is inspired by the verbal arguments of the "frozen niche variation hypothesis" (Vrijenhoek, 1979), in which each asexual clone has a genotype "frozen" to that of the sexual individual from which it arose. An increasing body of empirical evidence suggests that asexual clones often do represent a limited sample of the genetic variation within sexual populations, and that this constrains the phenotype of each clone to a narrower ecological niche (Vrijenhoek, 1979; Hebert *et al.*, 1988; Honeycutt & Wilkinson, 1989; Semlitsch *et al.*, 1997). There is further evidence to suggest that differences between the biotic or abiotic niches of competing clonal and sexual populations may result in coexistence (Case, 1990; Christensen *et al.*, 1992; Barata *et al.*, 1996; Fox *et al.*, 1996; Vrijenhoek & Pfeiler, 1997; Negovetic *et al.*, 2001).

Lomnicki (2001) has modelled the effect of niche breadth on the outcome of competition between sexual and asexual metapopulations competing for habitat patches. His model differs fundamentally from ours in two respects. Firstly, he considers only a resource of space which renews with consumer deaths, whereas we consider a consumable resource that renews independent of the consumer. Secondly, he measures the niche breadth of a metapopulation in terms of the proportion of total space available for colonizing, which then directly influences its intrinsic capacity for growth (i.e. colonization). Consequently, his model of a sexual metapopulation competing against an asexual invader with a narrower niche necessarily involves the asexual individuals having lower fitness. This is because their narrower niche gives them a lower intrinsic colonization capacity per capita, aside from any differences in fitness due to producing only females. Because the intrinsic growth capacities in Lomnicki's model are



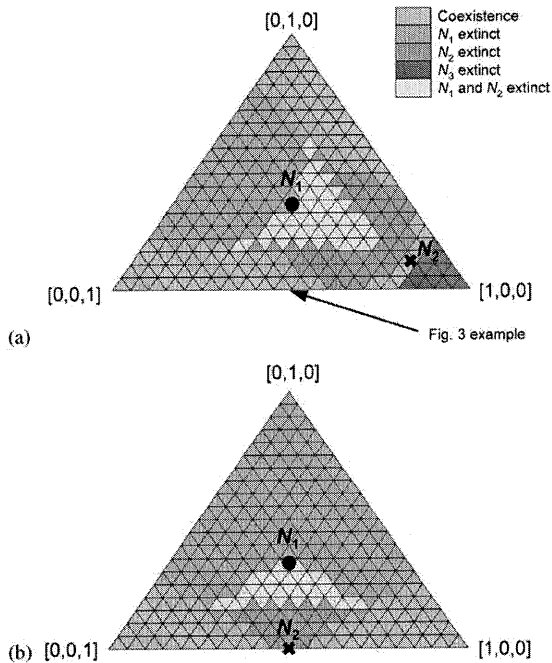


FIG. 4. The outcomes of invasion by two asexual clones for a range of clonal consumption strategies. Stable solutions are obtained by integrating eqns (3) over 5000 generations using the consumption matrix in eqn (8). They are plotted for the consumption strategy of clonal  $N_3$  at each cell mid-point, given the strategies for sexual  $N_1$  (dot) and clonal  $N_2$  (cross). Non-zero abundances are those greater than 0.0001, and the solutions agree with the analytical solutions. (a) The consumption strategy of  $N_2$  is  $c_{21} = c_{tot} \times 7/9$ ,  $c_{22} = c_{23} = c_{tot}/9$ . (b) The consumption strategy of  $N_2$  is  $c_{21} = c_{23} = c_{tot}/2$ ,  $c_{22} = 0$ . For both parts, the consumption strategy of  $N_1$  is  $c_{11} = c_{12} = c_{13} = c_{tot}/3$ . Other parameter values are as for Fig. 1(a).

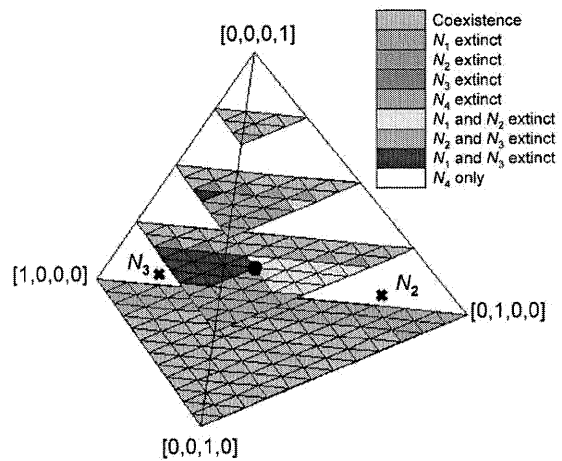


FIG. 5. The outcomes of invasion by three asexual clones for a range of clonal consumption strategies. Stable solutions are obtained by integrating eqns (3) over 5000 generations using the consumption matrix in eqn (9). They are plotted for the consumption strategy of clonal  $N_4$  given the strategies for sexual  $N_1$  (dot), and clonal  $N_2$  and  $N_3$  (crosses). The consumption strategy of  $N_4$  is illustrated at four values of  $c_{44} = 0, 0.25, 0.5$  and  $0.75$ . The values of  $c_{14}$ ,  $c_{24}$  and  $c_{34}$  are calculated in accordance with the condition that  $c_{41} + c_{42} + c_{43} + c_{44} = c_{tot}$ . Non-zero abundances are those greater than 0.0001, and the solutions agree with the analytical solutions. Other parameter values are as for Fig. 4.

directly proportional to niche breadths, he arrives at the tortologous result that the two-fold cost to sex in colonization capacity can be fully compensated only by a two-fold increase in niche breadth (measured in colonization capacity). In contrast, we are careful to give our competitors equal intrinsic fitness, by allowing them an equal total unitary rate of resource consumption,  $c_{tot}$  [e.g. in Table 1, intrinsic rates from eqns (1)  $r_1 = r_2$  given the condition that  $c_{11} + c_{12} = c_{22}$ , and  $k_1 = k_2$ ]. In this way we explore the influence of competition on the two-fold cost of males without confounding effects on fitness due to niche breadth alone. We find that sexual populations with high intrinsic growth capacity [high  $r_1/d_1$  in eqns (1)] need only slightly broader niches than asexual invaders to eradicate them [Figs 1(b) and (2)]. Niches that are much broader result in coexistence, since the two types then effectively occupy separate niches.

Clonal diversity may result from mutations within an asexual lineage, hybridization between clones and sexual sibling species or the repeated mutation to asexuality from a sexual population (Butlin *et al.*, 1999). Our analysis demonstrates that multiple clones represent no greater threat to the sexual population than single clones, provided some part of the resource niche of the sexual population is under-utilized by the clones. Under these conditions the frozen niche variation hypothesis alone may be responsible for coexistence between a sexual population and a diverse clonal population. This is possible because the clones compete not only with the sexual population for resources, but also amongst themselves (and intra-specifically: Doncaster *et al.*, 2000).

Relationships between genetic variation and phenotypic niche breadth are undoubtedly very complex and the Lotka–Volterra competition equations represent a simplification of this process. The Lotka–Volterra model of competition with multiple clones nevertheless clarifies the fundamental dynamics of the competition–growth trade-off that can sustain the sexual population. The analysis of multiple invasions is an important advancement on previous ecological simulations of the cost of sex (e.g. Bell, 1982; Case & Taper, 1986). It also concurs with

recent predictions about the advantage to sex of a high growth capacity, even though this will always be substantially less than the capacity for population growth of the clones (Doncaster *et al.*, 2000; Kerszberg, 2000). Interestingly, it is precisely amongst the lower orders of organisms with high growth capacity that asexual invasions are most likely to occur. Finally, the generic nature of Lotka–Volterra analyses permits applications to a wider range of systems than are possible from simulation models. For example the concept of resource exploitation can be expressed in terms of habitat colonization as opposed to prey consumption, in which case exactly the same model can apply to competition across a regional metapopulation.

The simulations of clonal invasions conducted by Weeks (1993) have shown how a sexual population will eventually be ousted by an assemblage of clones that exploit narrower niches if, between them, the asexual clones exploit almost the entire niche used by the sexual population. Our model allows this threshold to be calculated in terms of the competitive impact required by a clonal assembly to drive the sexual population to extinction. A sexual population can coexist with any number of clones, provided their combined competitive impact remains less than the impact of the clones on each other. Our analysis does not directly address the cumulative loss over time of the resource refuge for the sexual population, which Weeks (1993) predicts will prevent long-term coexistence. Nevertheless, we note that the accumulation of clones may be slowed or prevented by processes of competitive exclusion in the short term and evolutionary adaptation over longer time-scales.

It is one of the novel findings of our generic model that differences in niche breadth alone can be sufficient to competitively exclude asexual clones. Since this will happen as and when clones arise, it can prevent the asexual mutants from ever assembling multiple clones. For exclusion to occur, however, requires the sexual population to have exclusive access to a large resource whilst retaining a strong competitive impact upon the limiting resource of each arising asexual clone.

In all other circumstances, coexistence is a likely immediate outcome of competition with clones having relatively restricted competitive abilities, whether these are expressed in exploitation rates within an identical niche as in Doncaster *et al.* (2000) or in differences of niche breadth as here. Coexistence is also facilitated by inclusion of more than a single species of refuge prey (Fig. 5).

If the immediate outcome of competition is predicted to be coexistence with an asexual invader, ecological dynamics alone may be insufficient to explain the observed prevalence in the natural world of sexual over obligate asexual species. However, these dynamics do provide a time window for the sexual population to express other evolutionary advantages associated with greater genetic variation, such as escape from Muller's ratchet (Kondrashov, 1993). We therefore expect persisting clones may eventually be out-competed by the sexual population which has potentially greater fitness in the long term, and that the number of competing clones will not increase indefinitely over time. In similar vein, Peck *et al.* (1999) have shown how spatial structuring in a sexual population can sufficiently delay migration through it by an asexual invader for deleterious mutations to accumulate in the asexual population. It seems likely that a synergistic relationship between ecological processes and evolutionary adaptations will eventually prove the most convincing explanation for the ubiquity of sexual reproduction (e.g. West *et al.*, 1999). However, as Kover & Szathmari (1999) note, environmental models have yet to be incorporated into a pluralistic framework. The synergy between the frozen niche variation hypothesis and the varied benefits of sexual reproduction could be explored further by adding individual-based genetic algorithms to ecological models. At the cost of increased complexity, it might then be possible to quantify explicit contributions of the genome to niche breadth over ecological time-scales, and niche breadth to the genome over evolutionary time-scales.

We thank G. Bell and C. P. Please for clarification of key issues. This work was supported by an EPSRC studentship to GEP and a NERC grant to CPD.

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## Appendix A

### Solving Predator–Prey eqns (5)–(6)

We obtain an analytical solution to the case of a sexual population competing with one clone for a single prey species whilst retaining exclusive access to a second prey species. Solving the prey eqns (5) for zero net rates  $\dot{S}_1, \dot{S}_2 = 0$  gives prey equilibria as functions of predator abundance:

$$\begin{aligned} S_1^* &= k_1 \left( 1 - \frac{c_{11}}{a_1} N_1 \right), \\ S_2^* &= k_2 \left( 1 - \frac{c_{12} N_1 + c_{22} N_2}{a_2} \right). \end{aligned} \quad (\text{A.1})$$

Assuming the prey renew at fast time-scales relative to predator turnover, we can substitute  $S_1^*$  and  $S_2^*$  for  $S_1$  and  $S_2$  in eqns (6) to obtain predator rates at prey equilibrium:

$$\begin{aligned} \dot{N}_1 &= b_1(c_{11}k_1 + c_{12}k_2) \left[ 1 - \frac{(c_{11}^2k_1/a_1 + c_{12}^2k_2/a_2)N_1 + (c_{12}c_{22}k_2/a_2)N_2}{c_{11}k_1 + c_{12}k_2} \right] N_1 - d_1N_1, \\ \dot{N}_2 &= b_2c_{22}k_2 \left[ 1 - \frac{c_{22}N_2 + c_{12}N_1}{a_2} \right] N_2 - d_2N_2. \end{aligned} \quad (\text{A.2})$$

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Equations (A.2) are exactly equivalent to the Lotka–Volterra eqns (1), with  $r_i$ ,  $K_i$  and  $\alpha_{ij}$  defined in Table 1.

Solving for zero net rates:  $\dot{N}_1, \dot{N}_2 = 0$  gives the equilibrium abundance of each predator as a function of the abundance of the other:

$$\begin{aligned} N_1^* &= \frac{c_{12}k_2 + c_{11}k_1}{c_{12}^2k_1/a_1 + c_{11}^2k_1/a_1} \left( 1 - \frac{d_1}{b_1(c_{12}k_2 + c_{11}k_1)} \right) \\ &\quad - \frac{c_{12}c_{22}k_2/a_2}{c_{12}^2k_2/a_2 + c_{11}^2k_1/a_1} N_2, \\ N_2^* &= \frac{a_2}{c_{22}} \left( 1 - \frac{d_2}{b_2c_{22}k_2} \right) - \frac{c_{12}}{c_{22}} N_1. \end{aligned} \quad (\text{A.3})$$