

Dedicated to the memory of W. D. Hamilton

Competition, extinction, and the sexuality of species

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Received 25 January 2001, accepted 5 April 2001

Getz, W. M. 2001: Competition, extinction, and the sexuality of species. — *Ann. Zool. Fennici* 38: 315–330.

Considering the well-known two-fold cost of males associated with sexual reproduction, the maintenance of sex despite natural selection remains an enigma for population biologists. The prevalence of sex among eukaryotes is most commonly explained by hypotheses associated with either the purging of deleterious mutations, the generation of favorable gene combinations, the fixation of beneficial mutations, or, less frequently, ecological theories dealing with the coexistence of competing populations. Almost all these hypotheses ignore the fact that in stochastic environments, asexual populations exhibit higher rates of extinction than sexual populations because the latter generally exploit a wider spectrum of resources than their asexual counterparts. Here we develop a model to demonstrate, in populations where mutations from sexual to asexual reproduction are possible, that three reproductive phases — sexual, mixed, and asexual — naturally arise among competing sexual and asexual lines. The particular phase observed is related to the level of stochasticity in the environment experienced by the population complex in question (e.g. a partially competing group of congeneric species) and is a manifestation of the tension that exists between the reproductive superiority of asexual populations and their higher rates of extinction. I term this explanation the demographic balance hypothesis and suggest the endeostigmatid mites provide a suitable taxon for testing this hypothesis.

Introduction

Gene exchange among organisms may be as ancient as life itself. The evolution and maintenance of sexual reproduction in eukaryotes, however, are enigmas for both evolutionary and

population biologists. Biologists have found it difficult to explain how the demographic “two-fold cost of males” is maintained under natural selection. Specifically, how is sexual reproduction able to persist when the intrinsic reproductive rate of a sexually reproducing population is

half that of a clonally reproducing counterpart (e.g. *see* Williams 1975, Maynard Smith 1978, Bell 1982)? At issue is not how but why sex arose in eukaryotes (Kondrashov 1986, Charlesworth 1993) and not how but why reversals to asex occur and persist (Vrijenhoek 1993). Also at issue is the conundrum that while sexual reproduction is ubiquitous in animals, a number of higher taxa appear to have been exclusively asexual for many millions of years (Bell 1982, Maynard Smith 1986). In particular, genetic studies indicate that the bdelloid rotifers (class Bdelloidea) have abstained from sex for 30 to 40 million years (Welch & Meselson 2000).

Dating back to Weismann (1889), many hypotheses have been invoked to explain the importance of sexual reproduction. (For a critique of Weismann's original ideas *see* Burt (2000)). West *et al.* (1999), following Kondrashov (1993), broadly classify these hypothesis or explanations into two distinct categories: environmental and mutational. Both of these categories, though, are analyzed in either a genetic or natural selection, but not in a demographic, context.

Mutational hypotheses argue that deleterious mutations are more easily purged under sexual (amphimixis) than asexual (apomixis) reproduction. This results in what is loosely referred to as mutational meltdown in asexual lineages (Lynch *et al.* 1993). Recent data cast doubt, however, on the capacity of sexual reproduction to purge the genome of deleterious mutations (Kneightly & Eyre-Walker 2000).

Environmental hypotheses posit that either beneficial mutations, or at least favorable combinations of genes, accumulate more rapidly in amphimictically than apomictically reproducing populations (as reviewed in Kondrashov 1993, and West *et al.* 1999). Leigh Van Valen's (1973) "Red Queen's hypothesis" implies that the average fitness of individuals in a population is maintained at some characteristic fraction of optimal fitness for the species because the population's adaptive fitness landscape is continuously changing. This, in turn, implies that selection for new beneficial mutations and favorable combinations of genes is continually ongoing. The above mentioned characteristic fraction is going to be much closer to 1 under sexual than asexual reproduction because, as emphasized by

West *et al.* (1999), "Environmental models suggest that sex accelerates adaptation to a changing environment by creating new gene combinations ..."

Hamilton (1980), whose memory we honor in this volume, argued in the vein of the Red Queen that parasites and their hosts are involved in an "evolutionary arms race" in which sex is favored through the genetic variation it creates coupled with the fitness of rare host genotypes in the presence of parasites (*see also* Lively 1985, Ebert & Hamilton 1996, Hurst & Peck, 1996; but *see* Ladle *et al.* 1993). This and all the other environmental and mutational hypotheses reviewed by Kondrashov (1993) and West *et al.* (1999) do not explain why taxa, such as the bdelloid rotifers, have been asexual for many millions of years. If sex is advantageous for other species of rotifers, why is not advantageous for the asexual bdelloids?

The answer to this question could well lie in a currently neglected third category of explanations, namely purely ecological or demographic. From an ecological point of view, Bell (1982: p. 131) has argued that in a heterogeneous environment "... a single clone is unlikely entirely to supplant a diverse sexual population." This is not an argument that is ultimately caste in the context of natural selection but "... in terms of a contest between a clone which has the greater reproductive efficiency but a narrower ecological competence and an inefficient but broadly competent sexual population". Bell, inspired by a phrase in the concluding paragraph of Darwin's *Origin of Species*, refers to this explanation for the maintenance of asexual populations as the *tangled bank*.

Case and Taper (1986), and more recently Doncaster *et al.* (2000), used mathematical models to explore the plausibility of ecological explanations. Case and Taper, for example, analyzed the dynamical properties of three consecutive models at increasing levels of resolution with respect to the genotypic structure of the populations they represented: namely, a lumped model (no genotypic structure), a single locus genotype model (phenotype = genotype in this model), and a quantitative trait model. Their analysis revealed that sufficient ecological niche partitioning among phenotypes allows sexual

species to coexist and sometimes even supplant asexual species. On the other hand, Doncaster *et al.* (2000) used the very simple lumped two species Lotka-Volterra competition model with separate birth and death rate terms to demonstrate “the existence of a threshold growth rate for the sexual population, above which the invasion [of the asexual population] is halted by intraspecific competition.”

As West and Peters (2000) point out, Doncaster *et al.* (2000) essentially confirm Bell’s tangled bank hypothesis. The same is true of Case and Taper’s analysis, although they do find situations (regions of model parameter space) in which a sexual population completely displaces an asexual population and vice versa. Hence, Case and Taper do provide a possible explanation for the fact that some taxa are exclusively sexual, while others may be mixed or exclusively asexual. Note that analyses using population models lacking genetic or phenotypic structure, such as the first of Taper and Case’s three models and the Lotka-Volterra model used by Doncaster *et al.*, essentially reduce the analysis to a group selectionist argument. A model that is going to be used to address the ecological aspects of the sex versus asex conundrum needs to explicitly incorporate the fact that different phenotypes do not exploit the exact same ecological niche.

Williams (1975) raised the important question (p. 155): “Does the presence or absence of sexual reproduction in different taxa influence biotic evolution by altering rates of extinction, and if so, how?” Bell (1982) answers this question by pointing out that if sexual populations are less sensitive to loss of specific habitats than asexual populations, because a sexual population is likely to exploit a broader array of

habitats than an asexual population, then loss of a single habitat is more likely to lead to extinction of an asexual than a sexual population. The mechanism that I include in the model presented in this paper is more general than Bell’s. I allow habitats (represented by specific resource levels) to vary stochastically, but not necessarily disappear. This environmental stochasticity, together with the natural demographic stochasticity of populations (i.e. the natural sample variation associated with birth and death processes), results in asexual populations going extinct more often than sexual populations. Thus, it does not require the actual destruction of habitats to cause asexual populations to go extinct more often than sexual ones.

From a demographic point of view, a tension exists between the reproductive superiority of asexual populations and the fact that they are more likely than sexual populations to go extinct. With the aid of a model, I demonstrate below that this tension is sufficient to explain why we should expect asexual populations to dominate in relatively weakly stochastic environments, sexual populations in relatively highly stochastic environments, and the coexistence of the two in relatively moderate stochastic environments. I use the word relative because, in some taxons, the probability of extinction is greatly reduced through particular adaptations, such as the ability of bdelloid rotifer to survive dehydration and freezing (Örstan 1998). Interestingly, these three reproductive “phases” — asexual (low stochasticity), mixed (moderate stochasticity), and sexual (high stochasticity) — replicate a pattern observed in the distribution of sexual and asexual species in 27 genera of mites that are collectively known as the endeostigmata group (Norton *et al.* 1993, *see* Table 1). I refer

Table 1. Distribution of 79 sexual and 80 asexual species within 27 genera constituting the Endeostigmata group of mites (Acari).

	Purely asexual species	Mixed species (sexual/asexual)	Purely sexual species
Number of genera ^a	11	5	8
Mean number of species per genus	6.2	2.4/6	10.5

^a Three genera each containing a single asexual species are omitted because they are necessarily pure.

to the explanation provided by this tension between reproduction and extinction as the “demographic balance hypothesis.”

Returning to what West *et al.* (1999) refer to as a pluralist explanation for the maintenance of sex, demographic factors can always be added to obtain a more complete explanation. The critical question, however, is the relative importance of various processes in any given situation and whether, one particular process dominates in most situations. I will not answer this question but point out that, unlike most explanations relating to sexual reproduction, the demographic balance hypothesis is sufficient to explain why, in some taxa, either sexual or asexual reproduction dominates and, in other taxa, coexistence of the two strategies is apparent.

Model

In this section, a discrete time population model is presented that includes sufficient structure to explore issues relating to invasion, coexistence, and exclusion of sexual and asexual populations competing with different preferences and efficiencies for the same set of resources. This model is unrelated to models used in any previous studies and hence is more fully developed in the Appendix. A “symmetric” version of the model containing far fewer parameters than the more general model is presented here in the text under a number of simplifying assumptions. These assumptions, rather than reducing the general applicability of the analysis, allow us to focus on how the reproductive phase of the group of competing populations depends on the tradeoff between invasion (mutation) and extinction rates, where each of these rates is represented by a particular parameter in the model. (Note, the parameter that will be varied for the extinction rate is the one associated with the level of demographic stochasticity).

Deterministic symmetric phenotype model

Consider a sexually reproducing population that

consists of n identifiable phenotypes, each at density $x_i(t)$, $i = 1, \dots, n$, at time t . Suppose that each phenotype has the same heritability component h and the i^{th} phenotype has an asexual analogue that when extant has density $y_i(t)$, $i = 1, \dots, n$, at time t . Within each sexual phenotype and its asexual analogue, all individuals are considered ecologically identical (i.e. they are ecological homologues) in the way they compete for resources. For simplicity, consider a partition of a heterogeneous spectrum of resources into n components, such that the i^{th} component, with density at time t denoted by $z_i(t)$ $i = 1, \dots, n$, is preferred over all other components by the i^{th} ecological phenotype, whether sexual or asexual.

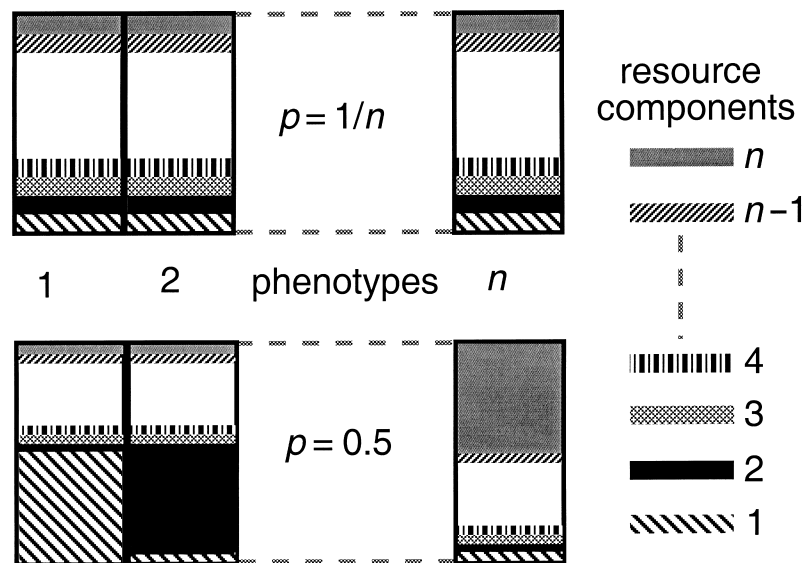
At any time t , from an ecological point of view, the population density of the combined sexual and asexual populations is given by the vector $\mathbf{x} + \mathbf{y}$, where $\mathbf{x} = (x_1, \dots, x_n)'$ and $\mathbf{y} = (y_1, \dots, y_n)'$, and the resource density is represented by the vector $\mathbf{z} = (z_1, \dots, z_n)'$. We assume that the rate at which an individual of phenotype i is able to ingest the resources it exploits (the resources must be converted to the same common currency — e.g. calories) is given by some function $\phi_i(\mathbf{x} + \mathbf{y}, \mathbf{z})$, $i = 1, \dots, n$.

Again, for simplicity, consider the case where all phenotypes have the same density-independent birth rate $b > 0$ and a resource-ingestion-dependent survival rate $s(\phi_i)$ expressed as

$$s(\phi_i) = \frac{\hat{s}a}{1 + (K / \phi_i)^\gamma}, \quad (1)$$

Here the parameter $K > 0$ scales the abscissa and the parameter $\gamma \geq 1$ determines how rapidly survivorship declines in the neighborhood of K (Getz 1996). The parameter a scales the ordinate axis and is expressed in terms of K and a maximum resource ingestion rate parameter $\delta > 0$ in a manner that ensures $s(\delta) = \hat{s}$. Specifically, $a = 1 + (K/\delta)^\gamma$ which ensures that the survival rate $s(\phi_i)$ increases monotonically on $[0, \delta]$ from its minimum value 0 to its maximum value \hat{s} . More generally, all the parameters in the function $s(\phi_i)$ could be indexed by i , but in the symmetric case treated here they are assumed to be the same for all phenotypes.

Fig. 1. A cartoon representation of the proportions of time each ecological phenotype (whether sexual or asexual) spends exploiting each of the n different resource components for the cases $p = 1/n$ (the proportions are all the same) and $p = 0.5$ (each phenotype spends half its time exploiting its preferred resource and divides the remaining time equally among the remaining $n - 1$ resources).



For each of the asexual phenotypes the change in population density from one unit of time (generation) to the next is modeled by the equation (cf. Eq. A5 in the Appendix)

$$y_i(t+1) = \frac{2\hat{s}ba}{1 + (K/\phi_i(\mathbf{x} + \mathbf{y}, \mathbf{z}))^\gamma} y_i(t), \quad i = 1, \dots, n, \quad (2)$$

where the constant 2 accounts for the fact that asexual females produce twice as many females per generation as their sexual ecological analogues and hence, all else being equal, their population compounds twice as fast each generation. The equations for the densities $x_i(t)$ are complicated by the fact that the sexual phenotypes interbreed. Assuming that all phenotypes are subject to the same heritability value h , and assuming that mating is random the equation is given by (cf. Eq. A5 in the Appendix)

$$x_i(t+1) = \frac{\hat{s}ba}{1 + (K/\phi_i(\mathbf{x} + \mathbf{y}, \mathbf{z}))^\gamma} \times \left(hx_i(t) + \left(\frac{1-h}{n} \right) x_T(t) \right), \quad i = 1, \dots, n. \quad (3)$$

All that remains is to specify the precise form of the resource extraction function $\phi_i(\mathbf{x} + \mathbf{y}, \mathbf{z})$.

In the context of a lumped population at density x exploiting a homogeneous population at density z , Beddington (1975) and DeAngelis *et al.* (1975) proposed the extraction function

$$\phi(x, z) = \frac{\delta z}{d + cx + z},$$

To keep the number of model parameters down to a minimum in generalizing this function to the situation considered here, assume that each individual independent of phenotype spends a proportion $1/n \leq p \leq 1$ of its time exploiting its

“preferred” resource and a proportion $0 \leq \frac{1-p}{n-1} \leq 1/n$ exploiting each of the remaining $n - 1$ “less preferred” resources. Note, if $p = 1/n$, then this latter inequality implies that each phenotype spends the proportion $1/n$ exploiting each of the remaining $n - 1$ resource components (this is the complete niche overlap case). Further, then the latter inequality implies the population does not exploit any of the remaining $n - 1$ resource components so that inter-phenotypic competition is 0 (this is the no niche overlap case) (see Fig. 1). Additionally, assume that individuals exploit all resources with equal inefficiency d , except for their preferred resource, which they exploit with inefficiency d/λ , ($\lambda > 1$ ensures

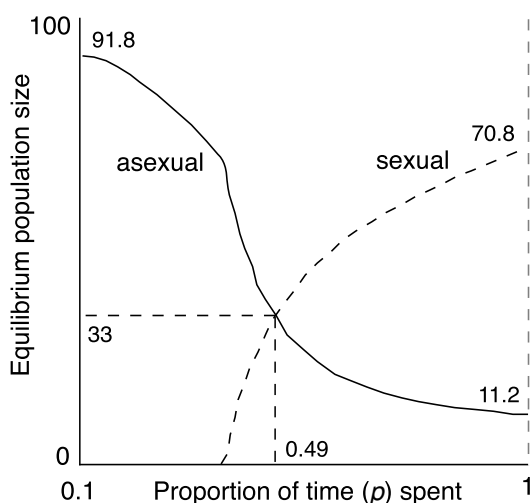


Fig. 2. The deterministic equilibrium size (units scaled by setting $K = 1$) of a sexual population competing with a single asexual clone for the baseline parameter set is plotted as function of the proportion of time p ($1/n \leq p \leq 1$ with $n = 10$) each phenotype spends on its preferred resource.

individuals are more efficient at exploiting their preferred resource).

With the above assumptions, and using the notation $x_T = \sum_{i=1}^n x_i$, $z_T = \sum_{i=1}^n z_i$ and $\pi = \left(\frac{p}{1-p}\right)(n-1)$, we can extend the above scalar form of the extraction function ϕ to obtain (see Appendix for more details)

$$\phi_i(x, z) = \delta \left(\frac{\pi z_i}{(n-1+\pi)d/\lambda + (x_T + (\pi-1)x_i) + z_T + (\pi-1)z_i} + \sum_{\substack{j=1 \\ j \neq i}}^n \frac{z_j}{(n-1+\pi)d + (x_T + (\pi-1)x_j) + z_T - z_j} \right) \quad (4)$$

Note that as $p = \frac{\pi}{(n-1+\pi)} \rightarrow 1$ it follows that

$$\pi \rightarrow \infty \text{ so that } \phi_i(x, z) \rightarrow \frac{\delta z_i}{d/\lambda + x_i + z_i}.$$

Baseline parameter values

Equations 2–4 constitute a deterministic model

of a sexual population with n phenotypes competing with n clonal populations where each clonal population is the ecological analogue of one of the sexual phenotypes. Generally, we can evaluate competition between the sexual population and a coalition of m ($1 \leq m \leq n$) asexual phenotypes by setting the initial conditions to $x_i > 0$ for at least some i , and $y_i > 0$, $i = 1, \dots, m$ and $y_i = 0$, $i = m+1, \dots, n$ (note, because the values of the parameters are independent of the phenotype, it makes no difference which set of $m-n$ initial clone densities is set to 0).

Despite all the simplifying assumptions, the model still has eight population parameters and n resource component inputs. Noting that the parameter K is a scaling constant that can be set to 1 without loss of generality, the following parameters were selected to be the baseline set for the analysis: $n = 10$, $h = 0.5$, $K = 1$, $\gamma = 2$, $\delta = 10$, $c = 10$, $d = 100$, and $z_i = 3$, $i = 1, \dots, 10$. The remaining parameters ensure that the model produces a stable coexistence equilibrium between the sexual and one of the asexual populations over the whole range of the niche partition parameter $p \in [1/n = 0.1, 1]$ (Fig. 2). Note that the model can produce chaos, particularly as the parameter γ increases in value (Schoombie & Getz 1998).

All numerical simulations of the model were run on an Apple G3 PowerPC using Berkeley Madonna, V. 8.0.1, (<http://www.berkeleymadonna.com/>). The code was checked by comparing numerical and analytical results for some of the simpler situations. For the more complicated situations, equilibrium solutions were obtained by running the model for several hundred generations until the solution was no longer changing for the desired number of significant digits. In the stochastic simulations, described below, the random number and normal distribution generator functions in Berkeley Madonna were used.

Stochastic extensions

Issues of coexistence and competitive exclusion of the sexual population and its parthenogenetic ecological homologues are greatly affected by the introduction of stochasticity into the model. Two kinds of stochasticity were included in the analysis. First, environmental stochasticity, was

included by treating the resource components z_i , $i = 1, \dots, 10$ as independent random variables. In stochastic runs, each of the components was drawn at each iteration of the model from a distribution generated by averaging the values of three uniformly distributed variables on $[0,6]$ (i.e. to clarify, within the same generation each of the resource components varies stochastically from the other resource components, and from one generation to the next each resource component itself varies stochastically). This procedure results in a symmetric bell-shaped distribution on $[0,6]$ that is more kurtotic (about -0.36) than a normal distribution, and has a mean of 3 and variance of 1.

Second, demographic stochasticity was included by multiplying the intrinsic growth rate by a normally distributed stochastic variable W with mean 1 and variance σ^2/x_r for the sexual population and σ^2/y_i for the i^{th} asexual population, but truncated so that all values of W less than 0.01 and greater than 3 were respectively set to 0.01 and 3. The implications of this choice are that: (i) $3\hat{b}$ is an upper bound under the most favorable of conditions, (ii) the population could not become negative, and (iii) the level of stochasticity is controlled by a variance parameter σ^2 with actual variance inversely proportional to population size (as it should be from sampling theory).

To obtain a more intuitive interpretation of the total level of stochasticity “perceived” by a sexual or asexual population existing in isolation in a particular stochastic environment, the coefficient of variation (CV) for the sexual and asexual populations was obtained from simulations for each population in isolation from the others over a period of 2000 generations (Table 3).

For extinction studies, populations were regarded as extinct and set to zero when the population size (x_r for the sexual population and y_i for the i^{th} asexual population) dropped below the value given by the “pseudo-extinction” threshold parameter θ . In reinvasion studies, populations that were 0 were set each time period to the value $\theta \times \text{INT}(V + \varepsilon)$ where INT denotes the integer part of the argument, and V is a uniformly distributed random variable on $[0,1]$. This approach implies that the random

values so obtained are less than θ with probability $1 - \varepsilon$, in which case the population size was reset to 0. Conversely, the random values so obtained are greater than or equal to θ with probability ε , in which case the system equations were used to calculate the next value of the invading population.

Simulation results

Coexistence equilibria

Numerical solutions of the deterministic Eqs. 2–4 indicate that when niche overlap is relatively strong (viz. $p < 0.37$ — see Fig. 2) a sexual population comprising of ten phenotypes is invaded and excluded by any of the ten clonal ecological homologues. Coexistence occurs, however, when niche overlap is relatively weak, and both populations have identical equilibrium levels when $p \approx 0.49$ (Fig. 2). As the degree of niche overlap is further reduced (i.e. $p > 0.49$), the sexual population becomes more dominant, but never excludes the asexual population. When niche overlap between ecological phenotypes is completely eliminated (i.e. at $p = 1$) the sexual and asexual equilibrium values are 70.8 and 11.2 respectively (Fig. 2). Though a sexual population can effectively compete against a single clonal line when niche overlap is zero, irrespective of the degree of niche overlap (i.e. value of p), the sexual population is always driven to extinction by a coalition of three or more clonal lines (Table 2).

Stochasticity and extinctions

Monte Carlo simulations were conducted for the case $p = 0.49$ that corresponds, in the absence of stochasticity, to the situation in which competing sexual and asexual populations coexist at the same equilibrium level of approximately 33 (Fig. 2). Setting the extinction threshold parameter value to $\theta = 0.01$ (i.e. approximately 0.03% of the equilibrium level of 33), both populations continue to coexist indefinitely for relatively small values of the demographic stochasticity parameter σ^2 even though environmental sto-

chasticity still produces moderate coefficients of variation in the sexual and asexual populations (Table 3). Virtually no extinctions occur over 1000 generations for $\sigma^2 = 2.0$, but for $\sigma^2 = 3.5$ the probability of survival of a clonal line for this period of time drops to 63% and for $\sigma^2 = 5.0$ to only 3% (Fig. 3), while the probability of survival of the sexual population remains at the 100% level in all three cases.

From the deterministic equilibrium (Table 2) and stochastic extinction (Fig. 3) results presented above, it is evident that at low levels of stochasticity coalitions of several clonal lines drive the sexual species to extinction, while at high levels of stochasticity coexistence of a sexual population with one or more clones is disrupted by the high rates of extinction of clonal lines.

Mutations and reproductive phases

The next step in the analysis is to allow sexual individuals to mutate into individuals that reproduce parthenogenetically (genetic aspects of this type of transformation are discussed in Bell (1982)). Such mutations are essentially equivalent to analyzing the invasion of a sexual popu-

lation by one more asexual clones that are ecological homologues of the various sexual phenotypes. We would not expect reverse mutations — that is, mutations from parthenogenetic to sexual reproduction — to occur because, in this case, contemporaneous mutations of parthenogenetic individuals to at least one male and one female are required. To level the playing field in our analysis of competition between a sexual population and a coalition of one or more clones, we consider invasions of a coalition of clones by a small group of sexually reproducing individuals. This invading group may originate from a remnant of the original sexual population that is now allopatric to the coalition of clones that competitively replaced it.

For simplicity, the rate at which asexual populations are reinvaded by sexuals is set equal to the rate at which sexuals are invaded by asexuals, irrespective of whether the latter is due to mutations or bona-fide invasions. The results, such as those in Table 4, are not critically dependent on these two rates being equal, or even close in value. Rather, the distribution of sexually reproducing species within taxa depends on the interplay of extinction and invasion rates, as well as competitive exclusion processes and the degree of stochasticity in the system.

Table 2. Deterministic equilibrium population sizes when model parameters have the baseline deterministic values $n = 10$, $h = 0.5$, $\hat{b} = 20$, $K = 1$, $\gamma = 2$, $\delta = 10$, $c = 10$, $d = 100$, $p = 0.49$ (i.e., $\pi = 8.75$), and $z_i = 3$, $i = 1, \dots, 10$.

Number of clonal lines competing with the sexual population	Equilibrium size of sexual population	Equilibrium size of each nonzero clonal line
0	57.7	N/A
1	33.0	33.2
2	31.2	11.8
3	extinction	27.4
4	extinction	22.5
5	extinction	19.2
6	extinction	16.8
7	extinction	15.0
8	extinction	13.5
9	extinction	12.3
10	extinction	11.3

Discussion

Equations 2–4 embody the underlying precepts of the *frozen niche variation* hypothesis (Vrijenhoek & Pfeiler 1997) and the closely related *frozen phenotypic variation* hypothesis (Jokel *et al.* 1997). These two hypothesis have respectively been shown to be compatible with the genetic structure of parthenogenetic populations of mollies (*Poeciliopsis* spp.) and snails (*Potamopyrgus anitpodarum*). Whether these competing sexual and clonal populations form an intraspecific or congeneric complex of competing populations, depends on how long the populations have been reproductively isolated and on our tendency to lump or split taxa. The above two hypotheses apply only to taxa in which parthenogenesis is able to arise from mutations or through interspecific hybridizations. Clearly the rates of such events are positive in taxa where parthenogenesis is observed, but appear to be zero in taxa, such as mammals, where both maternal and paternal genomes are needed for embryos to develop to term (Surani *et al.* 1984, Keverne *et al.* 1996).

Reproductive phases

The demographic balance hypothesis posits a “sexual phase” should occur whenever sexual to asexual mutation rates are relatively low or levels of stochasticity, and hence extinctions of asexual species is relatively high compared with sexual species (Table 4). With reducing levels of stochasticity, the asexual populations go extinct less often (Fig. 3) and it becomes increasingly likely that more than one asexual line exists at any point in time (Fig. 4). When the level of stochasticity has dropped far enough, a coalition of several asexual lines overwhelms and excludes the sexual population (Fig. 4 and Table 4) and we have an “asexual phase” for the taxonomic group in question. From the deterministic results (Table 2), an asexual phase must set in at some point as the level of stochasticity diminishes down to zero. The breadth of sto-

chastic levels supporting the transition between the sexual and asexual phases (i.e. the mixed phase in Table 4) depends on the invasion rate ϵ and on the extinction threshold θ .

Endeostigmatid mites

An example of sexual and asexual phases in related Acari genera is seen in the endeostigmatid mites, which are a collection of eleven closely related families totaling 159 species exploiting edaphic habitats and moss mats. Almost half the species are asexual (79 asexual and 80 sexual), yet five of the eleven families are purely asexual (although one of the families consists of only one species) while one is purely sexual. Also, within the remaining five mixed families, the majority of the genera are either purely sexual or asexual (Table 1). Of the twenty-four endeostigmatid genera containing more than one species, eight are purely sexual (10.5 species on average per genus), eleven are purely asexual (6.2 species on average per genus), leaving only five mixed (2.4 sexual and 6.0 asexual species on average per genus) (Table 1). Given the approximately equal number of sexual and asexual

Table 3. The coefficients of variation (CV) in the size of the sexual and asexual populations is tabulated here when environmental stochasticity is incorporated in the model and the level of demographic stochasticity in the model is given by the tabulated value σ^2 as listed below (see Methods section for more details).

Parameter σ^2	Sexual CV	Asexual CV
0.5	0.20	0.24
2	0.24	0.25
3.5	0.28	0.26
5	0.32	0.27
10	0.36	0.33 ¹⁾

¹⁾ This value is calculated only over the initial interval before the population goes extinct (i.e., drops to a level less than one thousandth of its isolation equilibrium level) which invariably happens before 1000 generations have transpired.

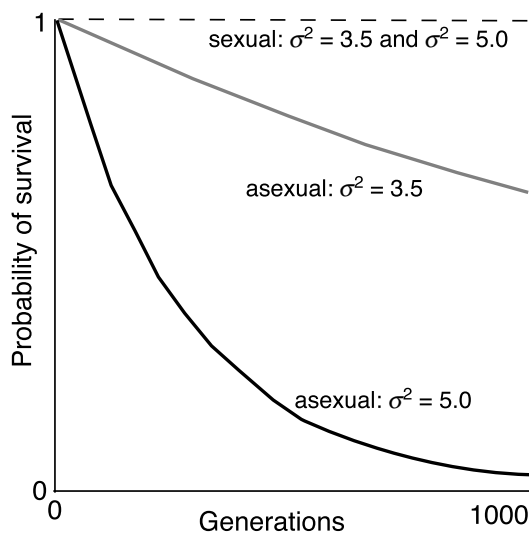


Fig. 3. Survivorship curves, obtained by averaging the results of one thousand Monte Carlo simulations over 5000 generations for the case of a single clonal line competing with a sexual population (initial conditions are $x_i(0) = 3$, $i = 1, \dots, 10$, $y_1(0) = 30$, and $y_i(0) = 0$, $i = 2, \dots, 10$), are plotted for the two increasingly stochastic cases $\sigma^2 = 3.5$ and $\sigma^2 = 5.0$ (i.e. increasing levels of demographic stochasticity but the same level of stochasticity in the underlying resources). Solid lines represent the asexual populations for the two cases (gray is $\sigma^2 = 3.5$ and black is $\sigma^2 = 5.0$) and the dotted line represents the sexual population which in both cases never goes extinct.

purely asexual group of six species is approximately $1/2^6 < 0.02$. Thus the probability of getting nineteen out of twenty-four genera at random to be purely sexual or asexual is exceedingly small.

Assuming that mutations for clonal reproduction arise equally frequently in all sexual species of endeostigmatid mites, the demographic balance hypothesis posits, as an explanation for the highly skewed distribution of purely sexual and asexual genera in Table 4 (c.f. Table 1), that purely asexual genera are found in environments that are less variable than the mixed genera which in turn are found in environments that are less variable than the purely sexual genera. Thus, the endeostigmatid mites provide a group of species that could be used to test the demographic balance hypothesis. To do so would require measuring the size of competing sympatric populations of the 27 species over enough generations to obtain reliable estimates of means and variances, and then comparing the coefficients of variation for sexual versus asexual species. Also, the coefficients of variation averaged across a group of sympatric species could also be compared with a spatially distinct group of species that represents a different reproductive phase.

species in the group, the probability of assembling at random a purely sexual group of ten species is approximately $1/2^{10} < 0.001$ or a

Distribution of parthenogenesis

The existence of sexual and asexual phases

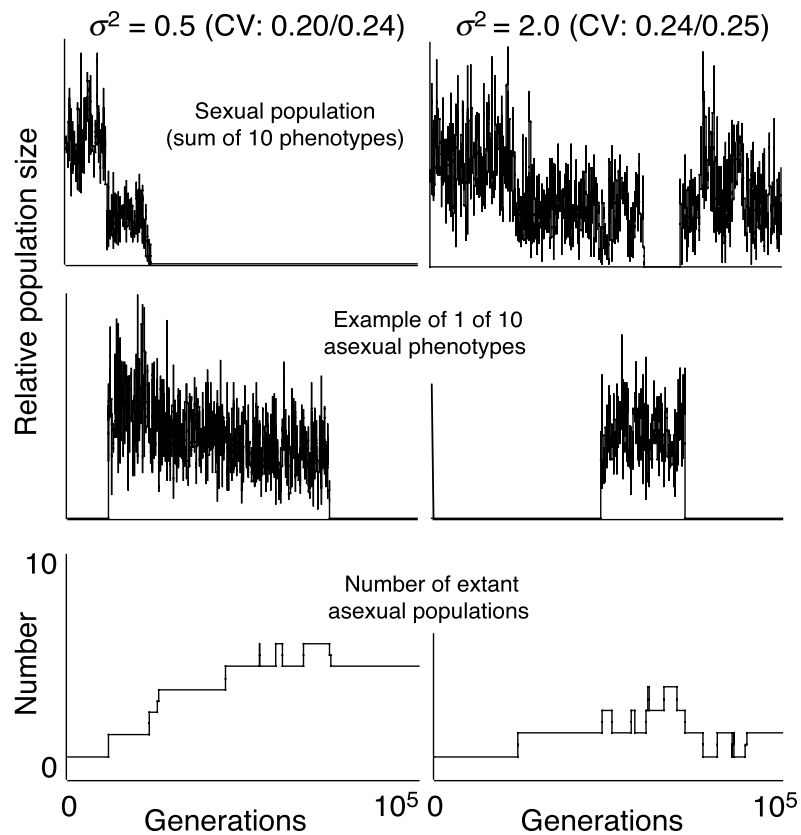
Table 4. The mean number of extant clonal lines and the likelihood of the sexual population being present (cf. Table 2) are listed for 3 separate simulations of each of the three different levels of stochasticity tabulated here (the invasion parameter is $\epsilon = 1 \times 10^{-4}$ and the extinction threshold is $\theta = 0.01$)^a. Also see Fig. 4 for some typical plots of the results.

CV: sexual/asexual (σ^2) Phase	0.20/0.24 (0.5) Asexual			0.24/0.25 (2.0) Mixed			0.36/0.33 (10) Sexual		
	1	2	3	1	2	3	1	2	3
Simulation run									
Sexuals ^b	0.0	0.0	0.0	0.9	0.5	0.8	1.0	1.0	1.0
Mean number of clonal lines	4.1	5.9	4.4	1.6	2.2	1.9	0.0	0.0	0.0

^a Mean values are calculated by sampling whether the sexual population exists and how many asexual clones exist every 100 generations during generations 50 000 to 100 000 of simulations with initial conditions $x_i(0) = 3$, $i = 1, \dots, 10$, $y_1(0) = 30$, $y_i(0) = 0$, $i = 2, \dots, 10$.

^b These entries represent the probabilities of the sexual population being present and are rounded to 1 decimal place with standard deviations omitted for clarity. Thus the 0's and 1's are not necessarily exactly 0 or 1.

Fig. 4. The size of the sexual population (top graph) and one of the ten asexual clones (middle graph), as well as the number of extant clonal lines (bottom graph) are plotted every 100 generations over 100 000 generations for one run of each of the two stochastic cases $\sigma^2 = 0.5$ and $\sigma^2 = 2.0$ (parameters: baseline deterministic values, invasion parameter $\varepsilon = 1 \times 10^{-4}$, extinction parameter $\theta = 0.01$, stochasticity of resources as described in the Methods; initial conditions: $x_i(0) = 3$ for $i = 1, \dots, 10$, $y_i(0) = 30$ and $y_i(0) = 0$ for $i = 2, \dots, 10$).



implies that the distribution of clonal lines should be clumped within genera when sexual populations are prevalent, or clumped within higher taxa if sexual populations have been excluded by coalitions of clonal lines for sufficiently long periods of time on evolutionary scales. The bdelloid rotifers represent the highest known taxonomic level that is exclusively asexual. In the bdelloid rotifers, however, the level of stochasticity that can be tolerated before transition to a mixed phase occurs may be greatly elevated by the fact that these rotifers have reduced extinction rates through adaptations that allow their eggs to survive dry or freezing conditions in anhydrobiotic forms and successfully rehydrate once the eggs are again in an aqueous environment (Örstan 1998).

Many examples of exclusively parthenogenetic families or genera exist in other taxa, including more complex invertebrates, particularly in the orders Acari (mites) and Hymenop-

tera (ants, bees, wasps, and sawflies). Haplodiploid genetic systems (diploid females develop from fertilized eggs and haploid males develop from unfertilized eggs) are common in Acari and obligate in Hymenoptera. This fact leads one to speculate that rates of transition from sexual to parthenogenetic reproduction are enhanced by haplodiploidy because these genetic systems permit the development of adults from unfertilized eggs. A comprehensive analysis evaluating the merits of this speculation is, however, beyond the scope of this paper.

Parthenogenesis occurs in at least 22 older vertebrata genera (Vrijenhoek *et al.* 1989), including the mollies (Vrijenhoek 1994) mentioned above, the salamanders *Ambistoma*, and whiptail lizards, *Cnemidophorus*. In the vertebrates, the origins of parthenogenesis appear to be through interspecific hybridization (Dawley 1989, Vrijenhoek 1989) rather than direct mutation. The model predicts that we should find

parthenogenetic species whenever extinction rates of parthenogenetic species do not overwhelm the rates at which parthenogenetic lines arise. The reason for the absence of parthenogenetic lineages in birds is not clear, but as in mammals, which we recall requires both parental genomes for successful embryogenesis (Surani *et al.* 1984, Keverne *et al.* 1996), may be related more to incompatibilities between parthenogenesis and embryogenesis than to rates at which clonal lines go extinct. Further, males have greater value in species where they play a critical role in rearing young, which appears to be more important in birds than any other class of vertebrates.

Conclusion

We should not expect any single factor to adequately explain the distribution of reproductive systems across all the eukaryotes. Rather, many processes and constraints at the genomic, physiological, behavioral, and ecological levels are likely to play a role. The most neglected process in explaining the current distribution of sexual and asexual species, however, is that asexual species have higher extinction rates in relatively stochastic environments. The power of this simple explanation is that it also predicts asexually dominated taxa in relatively stable environments. We see such domination at the genus and family taxonomic levels in endeostigmatid mites and at the class level in rotifers.

The ability of population models to predict observed frequencies of asexual species in various taxa will always be limited by the extraordinary complexity of real systems. Despite this, the analysis presented here provides for the first time an explanation of why, under a spectrum of conditions leading to different levels of stochasticity in populations, we might expect to see asexual, mixed, and sexual phases existing side by side in related taxonomic groups where mutations from sexual to parthenogenetic reproduction occur. This explanation represents a testable hypothesis in the case of the endeostigmatid mites, provided coefficients of variation can be estimated for the size of populations of the 27 species of mites constituting this taxonomic group.

Acknowledgements

I thank Simon Levin, Sir Robert May, and Michael Rosenzweig for supportive comments on an initial draft much different from this final version, George Barlow, Philip Starks, and David Wake for insightful comments and leads into the literature, and Peter Baxter, Paul Cross, Eran Karmon, James Lloyd-Smith, Jan Washburn, Stuart West, and Chris Wilmers for comments on various versions of the manuscript.

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Appendix

Deterministic Model

Let $x(t) \geq 0$ represent the density (numbers or biomass) of a population at time t . Assume population growth is regulated through intraspecific competition for a limiting resource $z(t) \geq 0$. If $\phi(x, z)$ is the amount of resources that each individual is able to extract from its environment during its reproductive life and $R(\phi)$ is the reproductive value of each individual at birth, then the model we develop here is based on elaborating the structure of R and ϕ in fundamental growth equation

$$x(t + 1) = R(\phi(x(t), z(t)))x(t), \quad (\text{A1})$$

and then structuring the population into competing phenotypes, each of which may or may not interbreed with other phenotypes.

In model A1, the units of time are generations. For a semelparous population, $R(\phi) = b(\phi)s(\phi)$, where $b(\phi)$ is the per capita birth rate (average number of progeny per adult) and $s(\phi)$ is the proportion of progeny that survive to reproduce while for an age-structured iteroparous population, the value of R and the length of a generation can be calculated from a stationary life table, assuming the population is at its stationary age distribution (Caswell, 2001). In the context of a homogeneous resource z , the notions of resource-dependent and ratio-dependent extraction rates are generalized by the Beddington-DeAngelis resource extraction function (Beddington 1975, DeAngelis *et al.* 1975; also Getz 1984, 1991, 1993)

$$\phi(x, z) = \frac{\delta z}{d + cx + z} \quad (\text{A2})$$

where $d > 0$, $c > 0$, and $\delta > 0$ respectively are extraction efficiency, interference competition, and maximum extraction rate parameters. Other forms for this functions can and have be used (May, 1981).

For simplicity, we assume $R(\phi) = bs(\phi)$, where $b > 0$ is constant, and for constants $0 < \hat{s} < 1$, $K > 0$, and $\gamma \geq 1$,

$$s(\phi) = \frac{\hat{s}a}{1 + (K/\phi)^\gamma}. \quad (\text{A3})$$

The constant a is expressed as $a = 1 + (K/\delta)^\gamma$ (recall the δ is the maximum extraction rate coefficient in function A2), which implies that the maximum survival rate is $s(\delta) = \hat{s}$. The parameter K scales the abscissa and the parameter $\gamma \geq 1$ determines how rapidly survivorship declines in the neighborhood of K (Getz 1996). Note that at $\phi = 0$ implies $s(0) = 0$ implying that all individuals die when no resources are consumed (from Eq. A2 holds whenever resources are absent, i.e., $z = 0$).

This formulation can be generalized in many ways to model several populations competing for a spatially, temporally, nutritionally, and physically (in terms of how easily they are handled and processed by the consumer) structured resource. Perhaps the most relevant way to characterize the resources is from the perspective of the consumers competing. For example, in the context of n competing populations, with density of population i denoted by x_i , $i = 1, \dots, n$, one perspective is to assume that we can structure the resources into n components z_i , $i = 1, \dots, n$, such that species i favors component i over all other components $j \neq i$, $j = 1, \dots, n$. If we use p_{ij} to denote the proportion of time

that individuals of type i spend exploiting resource component j , then it follows for each $i = 1, \dots, n$ that $p_{ii} \geq p_{ij} \geq 0, j = 1, \dots, n$ and $\sum_{j=1}^n p_{ij} = 1$. If we further assume that the degree to which individuals of type k interfere with an individual of type i in exploiting resource component j is proportional to the relative amount of time individuals of type k spend exploiting resource component j , then the extraction function A2, in the context of an individuals of type i exploiting all resource components, generalizes to (using the vector notation $\mathbf{x} = (x_1, \dots, x_n)'$ and $\mathbf{z} = (z_1, \dots, z_n)'$, where prime denotes vector transpose)

$$\phi_i(\mathbf{x}, \mathbf{z}) = \delta_i \sum_{j=1}^n \left(\frac{p_{ij} z_j}{d_{ij} + c_j \sum_{k=1}^n p_{ik} x_k + \sum_{k=1}^n p_{ik} z_k} \right). \quad (\text{A4})$$

Here $\delta_i > 0$ is the maximum resource extraction rate (we implicitly assume here that resources are substitutable so that no resource is limiting on its own), $c_j > 0$ is a constant that scales relative levels of interference with respect to the particular resource component being exploited, and the constants $d_{ij} \geq 0$ are the relative efficiencies with which individuals of phenotype i are able to exploit resource component j .

Generalizing Eq. A1 to a system of n -competing clonal populations is straightforward and takes the form $x_i(t+1) = b_i s_i(\phi_i(\mathbf{x}, \mathbf{z})) x_i(t)$. However, in the context of n interbreeding phenotypes, the model is complicated by the fact that we need to account for the frequency of mating types and heritability of phenotype. Let

$$q_{ijk} = \text{Pr}\{\text{phenotypes } j \text{ and } k \text{ have a progeny of type } i\}.$$

Then, if we do not distinguish between the order in which we list males and females, it follows that $q_{ijk} = q_{ikj}$. Now assume panmixis (i.e. random mating) and a 1:1 sex ratio. Then females of phenotype j , of which there are $x_j/2$, will breed with males of phenotype k in proportion to their representation x_k/x_T (where $x_T = \sum_{k=1}^n x_k$) to produce a total of $b_j q_{ijk} \frac{x_j}{2} \frac{x_k}{x_T}$ of progeny of type i , where b_j is the fecundity of females of phenotype j . Now, assuming the birth rates are independent of the amount of resources extracted, but survival rates are not, Eq. 1 generalizes to

$$x_i(t+1) = s_i(\phi_i(\mathbf{x}, \mathbf{z})) \sum_{j=1}^n \sum_{k=1}^n q_{ijk} (b_j + b_k) \frac{x_j(t) x_k(t)}{2 x_T(t)}, \quad (\text{A5})$$

where

$$s_i(\phi_i) = \frac{\hat{s}_i a_i}{1 + (K_i / \phi_i)^{\gamma_i}} \text{ and } a_i = 1 + (K_i / \delta_i)^{\gamma_i} \quad (\text{A6})$$

For the purposes of obtaining some insights into the how easily sexual and asexual populations are able to invade one another in terms of a few key parameters relating to the efficiency of exploitation,

the degree of overlap in resource utilization, and the heritability of phenotype in the sexual population, the following reduced parameter case can be investigated. First, assume all phenotypes

have the same heritability factor represented by a parameter $h \in [0,1]$ such that $q_{iii} = h + \frac{1-h}{n}$,

$q_{iji} = q_{ijj} = \frac{h}{2} + \frac{1-h}{n}$ for $j \neq i$ and $q_{ijk} = \frac{1-h}{n}$ for $j \neq i$ and $k \neq i$. (Note that these probabilities satisfy

the requirement that $\sum_{i=1}^n q_{ijk} = 1$). Second, assume all phenotypes in the sexual population are

demographically identical other than the fact that each is $\lambda > 1$ times more efficient in exploiting its preferred resource component, as well as having a preference $\pi > 1$ for its preferred resource component. In this case, it follows that there exist a set of positive parameters $c, b, s, \delta, \gamma, a$, and d such that for $i = 1, \dots, n$, we have $c_i = c, b_i = b, s_i = s, \delta_i = \delta, \gamma_i = \gamma$ (which implies $a_i = a$), $d_{ii} = d$, and

$p_{ii} = \frac{\pi}{n-1+\pi}$, while for $j \neq i, j = 1, \dots, n$, we set $d_{ij} = d/l$, and $p_{ij} = \frac{1}{n-1+\pi}$. (Note $\sum_{j=1}^n \pi_{ij} = 1$, as

required).

Using the fact that

$$\begin{aligned} \sum_{j=1}^n \sum_{k=1}^n p_{ijk} x_j(t) x_k(t) &= \left(h + \frac{1-h}{n} \right) x_i^2 + 2 \left(\frac{h}{2} + \frac{1-h}{n} \right) x_i(t) \sum_{\substack{k=1 \\ k \neq i}}^n x_k(t) \\ &+ \left(\frac{1-h}{n} \right) \sum_{\substack{j=1 \\ j \neq i}}^n \sum_{\substack{k=1 \\ k \neq i}}^n x_j(t) x_k(t) = h x_i(t) x_T(t) + \left(\frac{1-h}{n} \right) x_T(t)^2 \end{aligned}$$

models A5 and A6 simplify to yield Eq. 3 in the main text. Similarly, after defining $z_T = \sum_{k=1}^n z_k$, Eq.

A4 simplifies to yield Eq. 4.

For the case of noninterbreeding phenotypes is the parameters q_{ijk} in Eq. A5 clearly are $q_{iii} = 1, q_{iji} = q_{ijj} = 0$ for $j \neq i$ and $q_{ijk} = 0$ for $j \neq i$ and $k \neq i$. Once we take into account that parthenogenetic females produce females at twice the rate of sexually reproducing females, and change the names of the variables from x_i to y_i to indicate we are dealing the asexual rather than sexual phenotypes, Eq. A5 reduces to Eq. 2 in the main text.