



The Effects of Recurrent Clonal Formation on Clonal Invasion Patterns and Sexual Persistence: A Monte Carlo Simulation of the Frozen Niche-Variation Model

Stephen C. Weeks

American Naturalist, Volume 141, Issue 3 (Mar., 1993), 409-427.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at <http://www.jstor.org/about/terms.html>, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

American Naturalist is published by University of Chicago Press. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ucpress.html>.

American Naturalist
©1993 University of Chicago Press

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

THE EFFECTS OF RECURRENT CLONAL FORMATION ON CLONAL
INVASION PATTERNS AND SEXUAL PERSISTENCE: A MONTE
CARLO SIMULATION OF THE FROZEN NICHE-VARIATION MODEL

STEPHEN C. WEEKS*

Center for Theoretical and Applied Genetics, Cook College, Rutgers University,
New Brunswick, New Jersey 08903

Submitted July 1, 1991; Revised February 27, 1992; Accepted March 30, 1992

Abstract.—The interaction of sexual and asexual organisms in a heterogeneous environment was explored using a Monte Carlo simulation. The model was designed to address sexual persistence and the pattern of clonal invasion in a species that periodically produces clonal mutants. The parameters of the model were the mutation rate of outcrossed sexuals to obligate asexuality, the number of progeny per parent, the within-genotype niche width, and the carrying capacity for nine separate resources. The inclusion of recurrent clonal invasion due to meiosis-disrupting mutations drove the sexual species extinct in temporally stable environments, at a rate dependent on the mutation frequency, sexual niche breadth, and the relative magnitude of the number of progeny per parent and the carrying capacity. In simulations with uniform resource distributions, clonal invasion was distinctly nonrandom. The pattern of clonal invasion was "centripetal": mutant clones that captured or "froze" the rarely recombined (or marginal) sexual phenotypes were more successful initially than clones freezing frequently recombined (or central) sexual phenotypes. The long-term persistence of the sexuals was confined to simulations that included temporal resource fluctuations. In such instances, sexuals and asexuals coexisted in a mutation/extinction equilibrium, where asexuals were continually produced by mutation and lost by short-term random extinctions. Increased within-genotype niche width reduced the probability of clonal extinction and thus restricted the likelihood of sexual/clonal coexistence.

The search for benefits to sexual reproduction has led to the formulation of numerous hypotheses for short-term advantages of sex (for recent reviews see Stearns 1987; Michod and Levin 1988). Models invoking the benefits of genotypic diversity in spatially heterogeneous environments are especially attractive because we can empirically test them in a reasonable time frame. Such models assume that genetically variable populations can partition spatial and resource heterogeneity and therefore experience reduced intraspecific competition relative to their genetically homogeneous counterparts (Ghiselin 1974; Bell 1982).

To date, theoretical modeling of the spatial/resource variation hypothesis has followed the outcome of competition between a sexual population and one or more asexual clones (Maynard Smith 1976; Bell 1982; Case and Taper 1986; Koella 1988). Yet many natural asexual populations are combinations of numerous clones that appear to be recently derived from their sexual relatives (Bell

* Present address: University of Georgia, Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802.

Frozen Niche-Variation Model

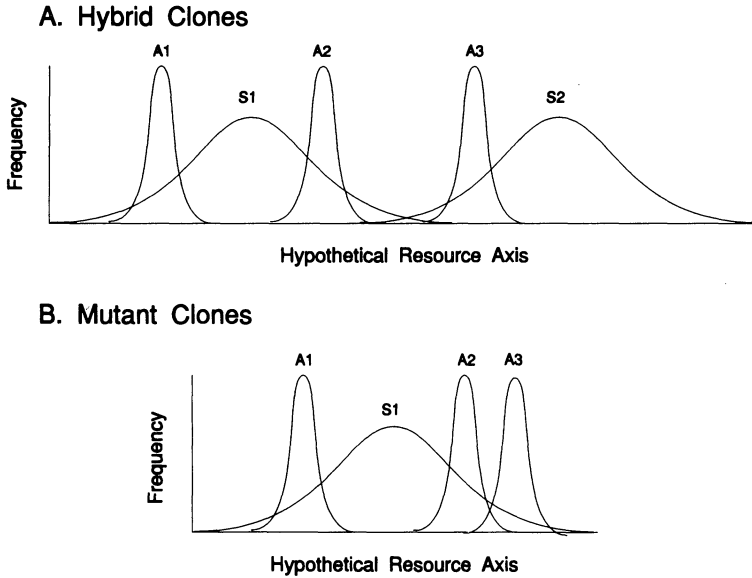


FIG. 1.—Hypothesized distribution of resource phenotypes in sexual and clonal populations. Clones are derived from the sexual population(s) either by (A) interspecific hybridization (hybrid model) or (B) one or more meiotic-suppressing mutations (mutant model). Clonal phenotypic distributions are represented by A1–A3, and sexual distributions are represented by S1–S2.

1982). The frozen niche-variation model, originally a verbal argument to explain the coexistence of multiple hybrid clones with their sexual ancestors (Vrijenhoek 1979, 1984), incorporates multiple clonal origins as a major component of sexual/asexual coexistence (hybrid model; fig. 1A). In this model, hybridization between congeneric sexual species disrupts meiosis and thereby “freezes” a single genotype that is subsequently inherited clonally. The model assumes that phenotypic expression of a new clonal genotype is narrower than that of its genetically variable sexual progenitors. The clone has a twofold reproductive advantage in habitats corresponding to its narrow phenotypic range because of the increased efficiency of asexual reproduction. Coexistence among such unisexual hybrids and their sexual ancestors is due to the sexuals’ capability to use a wider range of resources than any single clone can use. Multiple clones can coexist with sexuals as long as the total clonal niche does not completely overlap that of the sexual population.

Although the frozen niche-variation model was originally described in the context of hybridization, it can equally well be generalized to other asexual derivatives by incorporating nonhybrid clonal origins (mutant model; fig. 1B). Clones can be frozen from a single sexual population by mutations that produce unreduced eggs. Meiosis-disrupting mutations can either cause complete suppression

of meiosis (e.g., Hebert and Crease 1983) or pre- or postmeiotic reconstitution of the parental genotype (White 1978). Such mutants will freeze a single multilocus genotype, and its associated range of phenotypic expression, from that existing in the sexual population.

The recurrent production of clones, either through hybridization or mutation, appears to be a common theme in natural asexual populations (Uzzell 1964; Lowe and Wright 1966; Hewitt 1975; Uzzell and Darevsky 1975; Parker and Selander 1976; Schultz 1977; Vrijenhoek 1979; Jaenike et al. 1980, 1982; Turner 1982; Harshman and Futuyma 1985; Lowcock et al. 1987; Innes and Hebert 1988; Dessauer and Cole 1989; Goddard et al. 1989) and has yet to be specifically incorporated into theoretical treatments of the maintenance of sex. Periodic production of clones can potentially freeze all of the ecologically relevant phenotypic variation in reproductively efficient clones, which should lead to extinction of the sexual ancestor(s). Hence, repeated clonal formation poses serious problems for a sexual population (Bell 1982). Nevertheless, there is evidence for coexistence of sexual populations and recently derived clones in natural systems (Vrijenhoek 1979; Harshman and Futuyma 1985; Hebert et al. 1988; Honeycutt and Wilkinson 1989).

The possibility of recurrent clonal invasion raises three questions. First, how long can a sexual population avoid extinction under recurrent clonal invasion? Bell (1982) and Case and Taper (1986) predict that sexual populations can be driven extinct when competing with many ecologically distinct clones, but no previous work has clearly defined the expected time of sexual persistence in a population with recurrent clonal formation or explicitly explored the factors that might affect this persistence time. Second, are all sexual genotypes frozen in clonal mutants equally likely to persist, or are clones with some genotypes more successful at invading sexual populations than others? Finally, what are the conditions under which sexuals and clones can coexist? In this study, I use a Monte Carlo simulation of the frozen niche-variation model to investigate the effects of recurrent clonal formation on both clonal invasion and sexual persistence.

THE MODEL

The organisms were modeled as simultaneous hermaphrodites with nonoverlapping generations. Each individual was defined by a four-locus diallelic genotype. All loci were unlinked. The eight alleles combined to produce a one-dimensional, additive polygenic resource-use phenotype. Alternative alleles added either 0 or 1 units to the overall phenotype. Therefore, the total array of nine possible phenotypes ranged from 0 to 8, with a mean phenotype of 4. Each sexual individual invested equally in male and female gametes and produced N haploid eggs during its lifetime.

A fifth, unlinked locus controlled sexual reproduction. A sexual offspring had a probability M of having a dominant mutation at this locus that caused it to produce diploid, mitotic eggs and abandon male investment. Since asexual mutants were assumed to invest nothing in sperm production, they could produce twice as many progeny ($2N$) as a sexual individual, but all offspring possessed

the same genotype and phenotype as the individual in which the mutation originally arose.

All individuals coexisted in one heterogeneous habitat composed of nine different resource patches (0–8). Each resource had its own carrying capacity (K_0, K_1, \dots, K_8), which could range between 0 and 300 individuals per resource and could be either fixed or variable over time. The number of adults of each phenotype (T_i) was calculated assuming individuals of phenotype i could use a proportion $(1 - p)$ of K_i and $p/2$ of both K_{i-1} and K_{i+1} . To avoid edge effects, the number of adults with marginal phenotypes (T_0 and T_8) was calculated by assuming individuals of phenotype 0 could use a proportion $p/2$ of K_8 and vice versa for individuals of phenotype 8. For example, T_8 was calculated by considering a proportion $(1 - p)$ of K_8 , $p/2$ of K_7 , and $p/2$ of K_0 . The total adult population size (T_{tot}) was the sum of the adults of the nine phenotypes. Increasing p from 0 to 0.5 (the range examined) increased the within-individual niche width while decreasing the between-individual niche width in resource use (Roughgarden 1972). Both uniform and Gaussian resource distributions were considered, and resource abundance was either fixed or could vary over time. If a resource was available, it was assumed that all individuals with the corresponding phenotype would be able to find and compete for it.

Figure 2 shows the flow diagram of the simulation. The initial parameters for the simulation were: (1) the number of progeny per sexual parent, N , (2) the nine carrying capacities (K_0 – K_8) and whether they were fixed or varied over time, (3) the mutation rate from sexual to asexual, M , and (4) the within-individual niche width, p . An initial sexual population was generated by randomly assigning either 0 or 1 to all eight alleles for the T_{tot} parents. A gamete pool was generated from this adult population by creating $2N$ haploid gametes per sexual parent. The gametes were produced by randomly choosing one of the two alleles per locus at all four loci. A diploid progeny population was produced by randomly choosing, with replacement, $T_{\text{tot}}N$ eggs and an equal number of sperm from the gamete pool. Thus, a total of $T_{\text{tot}}N$ progeny were formed by this procedure with an average of N progeny per sexual parent.

An average of $MT_{\text{tot}}N$ offspring per generation was randomly chosen from the sexual progeny to become asexual mutants. These mutants froze the phenotypes that were associated with the sexual progeny in which the mutation arose. Back mutations, asexual to sexual, were not considered. Once a mutant arose, it was added to the asexual population of that phenotype.

The number of both sexual (S_i) and asexual (A_i) offspring of phenotype i was then compared to T_i . If $S_i + A_i$ was less than T_i , all offspring of that phenotype survived and became adults for the next generation. If $S_i + A_i$ was greater than T_i , the number of offspring in excess of T_i was randomly removed from the total progeny of that phenotype. The survivors were then used to reinitialize the adult arrays for the next generation (fig. 2).

Every 10 generations, the adult populations were enumerated. The data included the numbers of both sexuals and asexuals of each phenotype as well as the allele frequencies at the four phenotype-determining loci in the sexual population.

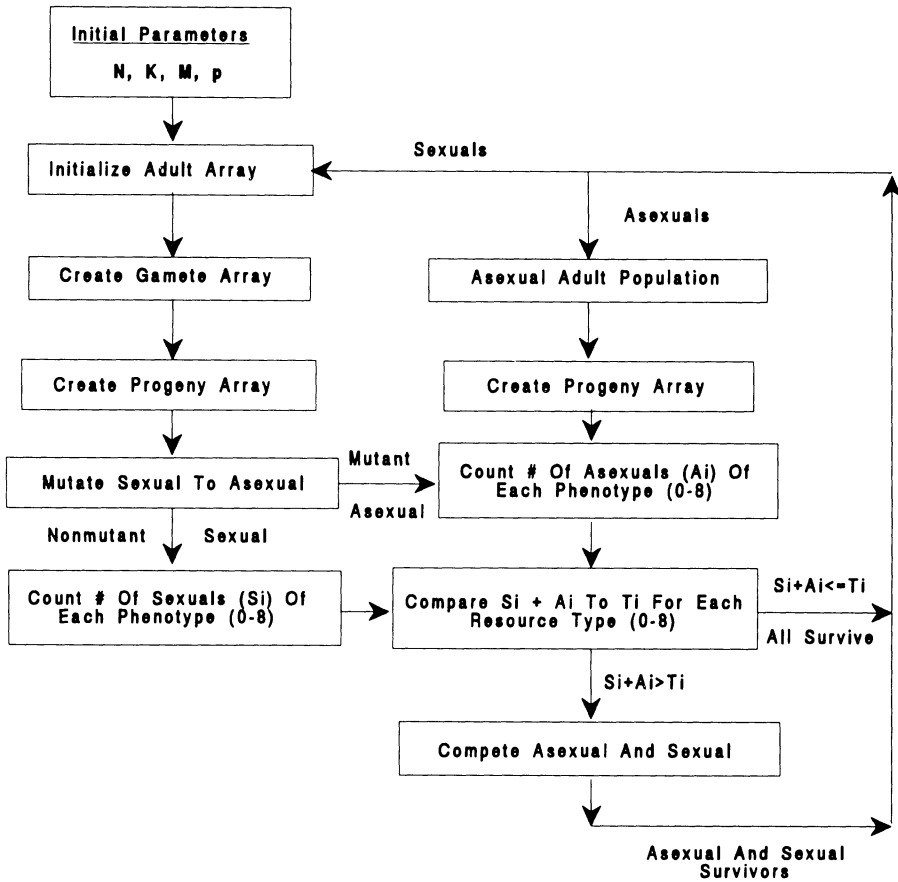


FIG. 2.—Flow chart of the Monte Carlo simulation routines. The variables are defined as follows: N , number of offspring per sexual adult; K , carrying capacity; M , sexual to asexual mutation rate; p , within-phenotype niche width; S_i , number of sexuals with resource phenotype i ; A_i , number of asexuals with resource phenotype i ; and T_i , maximum allowable number of individuals of phenotype i .

RESULTS

The first set of trials was run with $M = 0$, temporally invariant K_i , and a fixed number of clones to address sexual performance without recurrent clonal formation. As with previous models assuming competition of a sexual population with a fixed number of clones (Bell 1982; Case and Taper 1986; Koella 1988), the sexual population was able to persist because of its use of uncontested resources. Sexual frequency was influenced by the number of competing clones, with increased clonal number resulting in decreased sexual abundance. These results were consistent with previous models. Later trials addressed clonal invasion patterns and sexual persistence assuming a constant probability of clonal formation.

The first set of trials with $M > 0$ was performed with fixed K_i to determine the

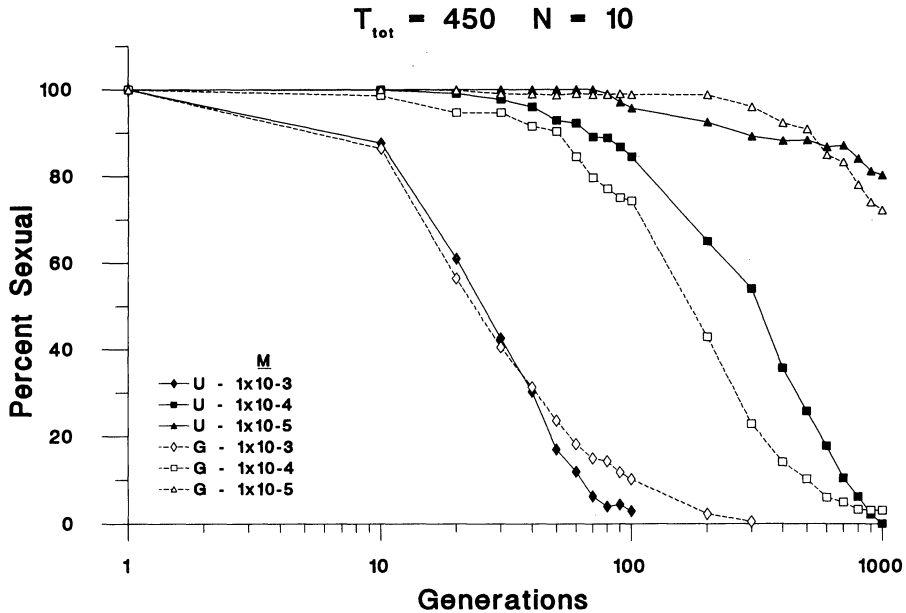


FIG. 3.—Persistence times of sexual populations of different sexual to asexual mutation rates, M , in habitats with uniform and Gaussian resource distributions. Total adult population size, T_{tot} , and number of offspring per sexual adult, N , were set at 450 and 10, respectively. Results of trials assuming a uniform resource distribution ($K_0 = K_1 = \dots = K_8 = 50$) are represented by *solid lines* and *filled symbols*, whereas results of trials assuming a Gaussian resource distribution ($[K_0-K_8] = [10, 20, 40, 85, 140, 85, 40, 20, 10]$) are represented by *dashed lines* and *open symbols*.

persistence time of a sexual population in a temporally stable environment, given various combinations of N , K_i , M , and p , and to examine clonal invasion patterns (see below). The second set of trials explored the effects of a temporally variable environment on sexual/clonal coexistence. Asexual replacement rates were sometimes quite prolonged. Therefore, exact equilibrium values and persistence times were not calculated to reduce computational costs. Sexual/clonal coexistence was conservatively defined as a zero slope of a regression of the percentage of sexuals on generation time for the last 200 generations examined (800–1,000). All results reported below are the means of 10 or more trials per set of initial conditions. Most of the simulation trials were examined at high mutation rates ($M = 10^{-3}$ to 10^{-5}) to reduce computation time. Lower mutation rates yielded qualitatively similar conclusions extended over a longer time frame.

Rate of Sexual Replacement

The effect of recurrent clonal formation on sexual persistence times was evaluated under conditions of temporal resource stability. Increasing the asexual mutation rate (M) by an order of magnitude led to a corresponding decrease in sexual persistence by approximately one order of magnitude at a fixed N and K_i (fig. 3).

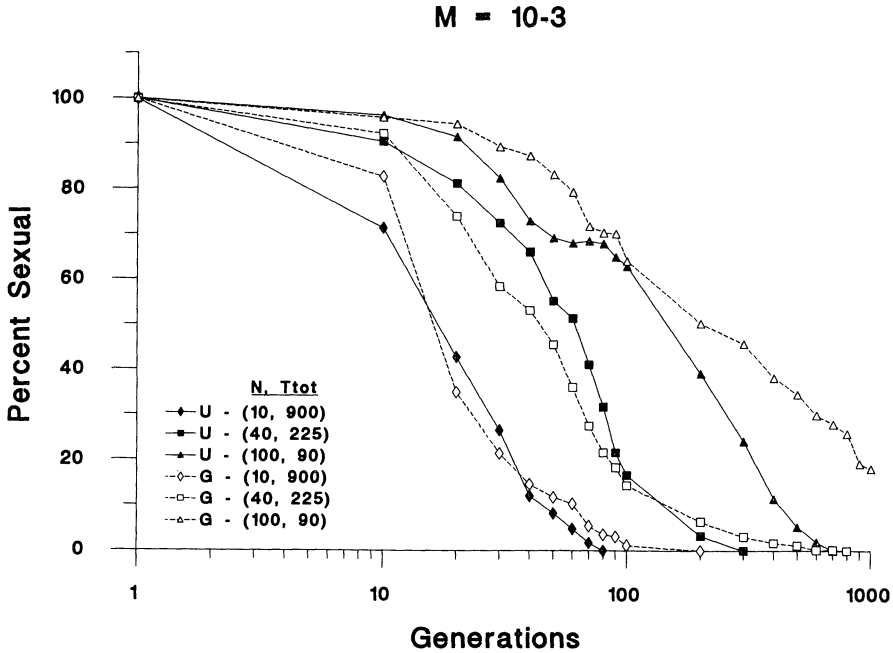


FIG. 4.—Persistence times of sexual populations of varying combinations of N and T_{tot} . The product $NT_{\text{tot}}M$ was held constant at 9. The parameter M was set at 1×10^{-3} , while N and T_{tot} were reciprocally varied. Results of trials with uniform resources are represented by *solid lines and filled symbols*, whereas results of trials assuming a Gaussian resource distribution are represented by *dashed lines and open symbols*. The various carrying capacities were as follows: *filled diamonds*, $K_0 = K_1 = \dots = K_8 = 100$; *filled squares*, $K_0 = \dots = K_8 = 25$; *filled triangles*, $K_0 = \dots = K_8 = 10$; *open diamonds*, $[K_0-K_8] = [20, 40, 80, 170, 280, 170, 80, 40, 20]$; *open squares*, $[K_0-K_8] = [5, 10, 20, 43, 70, 43, 20, 10, 5]$; *open triangles*, $[K_0-K_8] = [1, 2, 4, 9, 14, 9, 4, 2, 1]$.

The shape of the resource distribution (uniform vs. Gaussian) had little overall effect on sexual persistence (fig. 3). Variation in the resource use parameter, p , did not significantly affect sexual persistence in environments with either uniform or Gaussian resources. Increasing N while reciprocally decreasing K_i increased sampling error associated with choosing adult survivors, which did lengthen sexual persistence times (fig. 4). The sexuals could persist for thousands to tens of thousands of generations in simulations with low mutation rates and high N/K . The rate of sexual replacement decreased as sexuals neared extinction (figs. 3, 4) because, as the sexuals became increasingly scarce, the likelihood of a clonal mutant's arising was so low that the remaining sexuals could "hang on" to their resource type until an asexual finally mutated in that group. When an asexual mutant finally did arise, the sexuals were quickly driven to extinction.

Clonal Invasion Pattern

In the trials with Gaussian resource distributions, clonal success was independent of resource phenotype (table 1). However, in the trials with uniform re-

TABLE 1
RELATIVE CLONAL SUCCESS OF THE NINE PHENOTYPES

	PHENOTYPE								
	0	1	2	3	4	5	6	7	8
Gaussian:									
Maximum <i>K</i>	10	20	40	85	140	85	40	20	10
Generation:									
10	10 (0)	20 (0)	40 (0)	85 (1)	136 (11)	83 (7)	40 (0)	20 (0)	10 (0)
40	9 (3)	18 (5)	40 (0)	75 (21)	121 (40)	81 (14)	40 (0)	19 (5)	8 (3)
70	9 (3)	18 (6)	36 (11)	67 (28)	84 (50)	81 (12)	38 (7)	18 (5)	8 (4)
100	8 (4)	18 (5)	34 (13)	62 (30)	78 (52)	70 (26)	37 (10)	18 (5)	8 (4)
400	5 (5)	9 (10)	13 (19)	2 (4)	3 (7)	2 (4)	13 (19)	12 (10)	3 (5)
700	3 (5)	6 (10)	1 (2)	1 (2)	1 (2)	0 (1)	1 (2)	6 (10)	3 (4)
1,000	3 (5)	6 (10)	0 (1)	0 (0)	0 (0)	0 (0)	0 (1)	2 (6)	3 (4)
Uniform:									
Maximum <i>K</i>	50	50	50	50	50	50	50	50	50
Generation:									
10	42 (20)	50 (0)	48 (5)	50 (0)	49 (2)	50 (0)	50 (0)	50 (0)	50 (0)
40	42 (20)	50 (0)	45 (12)	50 (0)	50 (0)	50 (0)	50 (0)	43 (16)	26 (26)
70	34 (25)	43 (17)	44 (14)	50 (0)	50 (0)	50 (0)	46 (8)	43 (18)	19 (24)
100	34 (25)	30 (23)	43 (11)	40 (17)	50 (0)	50 (0)	41 (14)	36 (21)	18 (25)
400	18 (25)	13 (20)	20 (24)	13 (17)	19 (18)	37 (21)	28 (24)	11 (19)	9 (20)
700	20 (27)	3 (8)	20 (27)	6 (10)	9 (11)	25 (25)	23 (24)	10 (22)	10 (22)
1,000	0 (0)	0 (0)	18 (28)	0 (0)	2 (3)	17 (29)	4 (7)	0 (0)	0 (0)

NOTE.—The values are the mean number of sexuals of each phenotype averaged over 10 trials. Values in parentheses are 1 SD of the means. Model parameters were set at the following values: $T_{\text{tot}} = 450$, $N = 10$, $p = 0$, and $M = 10^{-4}$. Maximum *K* designates the maximum carrying capacity for each phenotype.

sources, clonal mutants with “marginal” or rarely recombined phenotypes (0, 1, 7, and 8) were more successful in early colonization than clones with “central” or commonly recombined phenotypes (3, 4, and 5; table 1). Clones freezing either end of the distribution (0 and 1 or 7 and 8) would be successful initially (table 1). Which of the two ends was initially colonized depended on initial conditions, which was reflected in the higher variance in the marginal resources in the early generations. The asexual mutants with the central phenotypes became increasingly successful as the total sexual population was progressively reduced. Thus, asexual invasion typically progressed from the marginal toward the central phenotypes when resources were uniformly distributed.

The “centripetal” asexual invasion pattern in simulations with uniform resources suggested differential sexual resistance as a function of phenotypic frequency. To test this prediction, several trials were run with $M = 0$ with both uniform and Gaussian resource distributions to examine the equilibrium number for a single mutant clone freezing each of the nine phenotypes. The parameters N and T_{tot} were set at 20 and 450, respectively. The simulations were started with 10 individuals of a single clone and 440 sexual adults. Under no conditions did the clones completely exclude the sexuals of the corresponding phenotype (fig. 5C, D). In the trials with uniform resources, the increased sampling error for central phenotypes associated with superimposing a normal progeny distribution

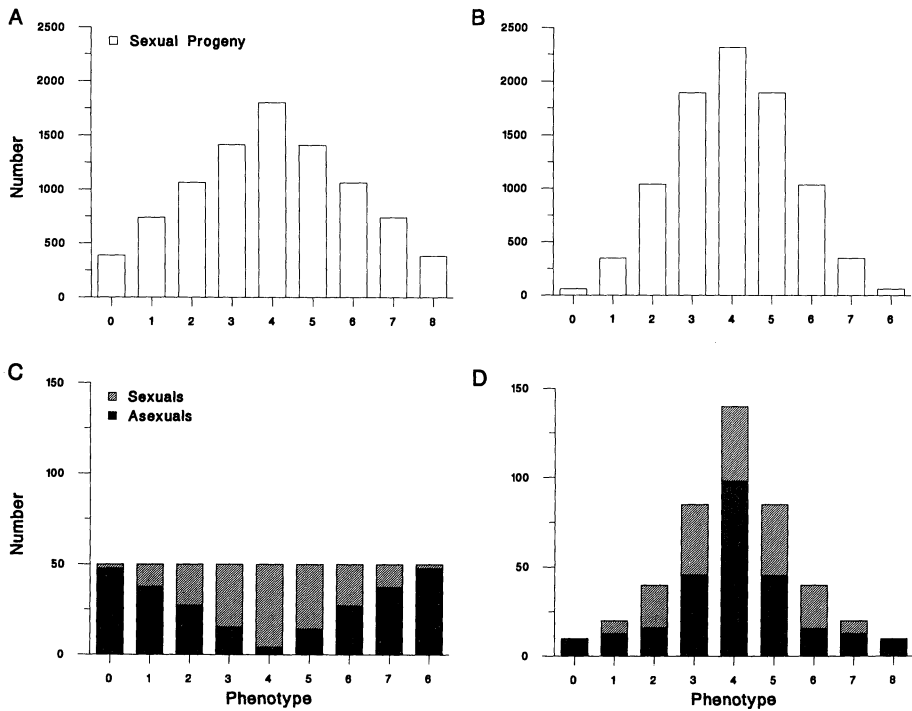


FIG. 5.—Sexual progeny distributions and asexual equilibrium frequencies in trials with uniform and Gaussian resource distributions. The progeny distributions (A, B) were generated in trials with $M = 0$ and assuming no competing clones. See text for an explanation of the determination of the asexual equilibrium values. These values are the equilibrium proportions averaged across 180 generations (20–200) for each of 10 trials. Generations in which the clone went extinct were not used for determination of equilibrium frequencies. The total population size (T_{tot}) was set at 450 for all trials; A and C represent the results of the uniform resource trials with $K_0 = K_1 = \dots = K_8 = 50$; B and D represent the results of the Gaussian resource trials with $[K_0-K_8] = [10, 20, 40, 85, 140, 85, 40, 20, 10]$. Random clonal extinctions occurred only in trials with uniform resources (C): 2 of 10 trials for clones of phenotype 3, 10 of 10 trials for clones of phenotype 4, and 5 of 10 trials for clones of phenotype 5.

(fig. 5A) on a uniform resource distribution (fig. 5C) led to random extinction of clones with phenotypes 3, 4, and 5. In fact, the asexuals randomly drifted to extinction in less than 200 generations in all 10 trials initialized with clones of phenotype 4 in simulations with uniform resource distributions. Thus, clones with central phenotypes were unsuccessful at invading central resources because of high competition and random clonal extinction, under conditions of uniform resources.

In the trials with a Gaussian resource distribution, the progeny array (fig. 5B) more closely matched the resource array (fig. 5D). This concordance of progeny and resource distributions reduced overall sampling error and resulted in no extinctions in any of the nine phenotypic clones. Although sexuals made up a greater

proportion of the total in the central relative to marginal phenotypes (fig. 5D), they were never the numerically dominant type, as they were for the central phenotypes in the uniform case (fig. 5C). Nevertheless, these differences in invasion patterns did not affect overall sexual persistence times (figs. 3, 4).

Sexual/Clonal Coexistence

No combination of N , K_i , M , and p in simulations with either uniform or Gaussian resource distributions allowed for sexual/clonal coexistence in habitats with temporally stable resources. Increased sampling error did prolong sexual persistence (fig. 4) but was insufficient to allow stable sexual/clonal coexistence.

The possibility of sexual/clonal coexistence was further explored in environments that combined temporally fluctuating resources with sampling error. In these trials, the nine carrying capacities were randomly varied every generation. Since previous trials indicated that shape of the resource distribution had little effect on sexual persistence times, uniform resource distributions were used for simplicity. The parameter K_i ranged from 0 to 100, and was separately determined for each of the nine resources in each generation. The K_i 's for each patch were determined by choosing, with a probability of q , U units of carrying capacity L times. Thus, $K_i = U \times Y$, where Y is defined as a binomial random variable with number of trials = L and probability of success = q (i.e., mean (K_i) = $U \times L \times q$ and $\text{var}(K_i) = U^2 \times L \times (1 - q) \times q$). For example, values of $U = 20$, $L = 5$, and $q = 0.5$ would require five draws of 20 units of carrying capacity with a probability of 0.5 for each draw, to produce a mean carrying capacity of 50 units and a probability of extinction (a total draw of zero units) of 0.03125 (0.5^5) per generation, per resource. The parameter q was held constant at 0.5 and the product $U \times L$ was chosen to be at or near 100. Therefore, mean K_i was set at or near 50 for all trials, whereas the variance in K_i was set at five levels ($[U, L] = [7, 14], [10, 10], [14, 7], [20, 5], \text{ and } [50, 2]$). These levels had corresponding extinction probabilities of 1/16,384, 1/1,024, 1/128, 1/32, and 1/4 per resource per generation, respectively.

There were three outcomes in these simulations: (1) the asexual population outcompeted the sexual population and then was driven extinct when its resource base fluctuated to zero, (2) the sexual population was resistant to invasion by the asexual mutants, and the two reproductive types existed in a mutation/extinction equilibrium, with asexuals arising through mutation and persisting until their resources fluctuated to zero, and (3) both sexual and asexual populations were driven extinct by resource fluctuations. Which of the three outcomes applied was principally dependent on the mutation rate, M , the within-genotype niche width, p , and the likelihood of resource extinction, quantified by the ratio U/L (table 2; fig. 6). When the within-genotype niche width was low ($p = 0$), sexual/clonal coexistence was found over a range of M and U/L (table 2A). At low to intermediate U/L and with high asexual mutation frequency, asexuals would outcompete sexuals in all but the most fluctuating environments ($[U, L] = [50, 2]$) (table 2A). In these trials, the resulting clonal lines eventually would be driven extinct by resource fluctuations. At intermediate U/L and low asexual mutation frequency, the asexuals would be driven extinct nearly as quickly as they arose, producing

TABLE 2

PROPORTION OF SEXUALS AND GENE DIVERSITY (H) AT 1,000 GENERATIONS FOR VARIOUS COMBINATIONS OF ASEQUAL MUTATION RATE (M) AND TEMPORAL RESOURCE FLUCTUATION ($[U, L]$)

M	$[U, L]$				
	[7, 14]	[10, 10]	[14, 7]	[20, 5]	[50, 2]
A:					
10^{-2}	X	X	X	X	.73 (.12) S^* $H = .38$
10^{-3}	X	X	X	.04 (.13) D $H = .037$.96 (.08) S $H = .48$
10^{-4}	.04 (.06) D $H = .12$.16 (.21) D $H = .11$.81 (.14) S $H = .47$.94 (.07) S $H = .50$	1.00 (.00) S^\dagger $H = .43$
10^{-5}	.78 (.10) S $H = .49$.96 (.08) S $H = .50$.99 (.04) S $H = .50$	1.00 (.00) S $H = .50$	1.00 (.00) S^\ddagger $H = .44$
B:					
10^{-2}	X	X	X	X	X
10^{-3}	X	X	X	X	X
10^{-4}	.13 (.04) D $H = .01$.01 (.04) D $H = .00$.02 (.05) D $H = .01$.06 (.08) D $H = .02$.85 (.09) S $H = .47$
10^{-5}	.77 (.16) D $H = .47$.80 (.10) D $H = .49$.73 (.19) D $H = .48$.80 (.10) D $H = .48$.99 (.03) S $H = .49$

NOTE.—The average proportion of sexuals is shown on the top line of each row with the SD in parentheses. Average genetic diversity, H (Nei 1975), is shown on the second line of each row. The symbols are defined as follows: X = sexual extinction in all 10 replicates by generation 1,000; S = stable coexistence of sexuals and clones (see text for definition of stable coexistence); D = declining sexual population (i.e., no stable coexistence). A, $p = 0.0$ and $N = 10$; B, $p = 0.5$ and $N = 10$. In each of the sections A and B, combinations of mutation rate and temporal resource fluctuations that led to sexual extinction or declining populations are shown above the dotted line, while combinations that led to stable coexistence are below the line.

* Extinction of all individuals by 700 generations in one replicate trial.

† Extinction of all individuals by 700 generations in one and by 800 generations in a second replicate trial.

‡ Extinction of all individuals by 500 generations in one replicate trial.

an equilibrium between mutation and extinction. At high U/L ([50, 2]), the clones were extinguished almost immediately after their origination at all levels of M , but the resources were so unstable that genetic diversity in the sexual population was slowly eroded (table 2). In fact, several trials resulted in complete extinction of both the sexual and asexual populations (table 2A).

When the within-genotype niche width was increased ($p = 0.5$), sexual/clonal coexistence was restricted to low values of M and high U/L (table 2b). The increased within-genotype niche breadth necessitated increased resource fluctuations for sexual/clonal coexistence (table 2B; fig. 6) but also allowed the sexual population to be more robust to resource fluctuations (none of the sexual populations were driven extinct in any trial studied). Thus, although increased within-individual niche breadth required increased environmental fluctuations for sexual/clonal coexistence, the sexuals were able to withstand these increased fluctuations due to their correspondingly increased niche breadth.

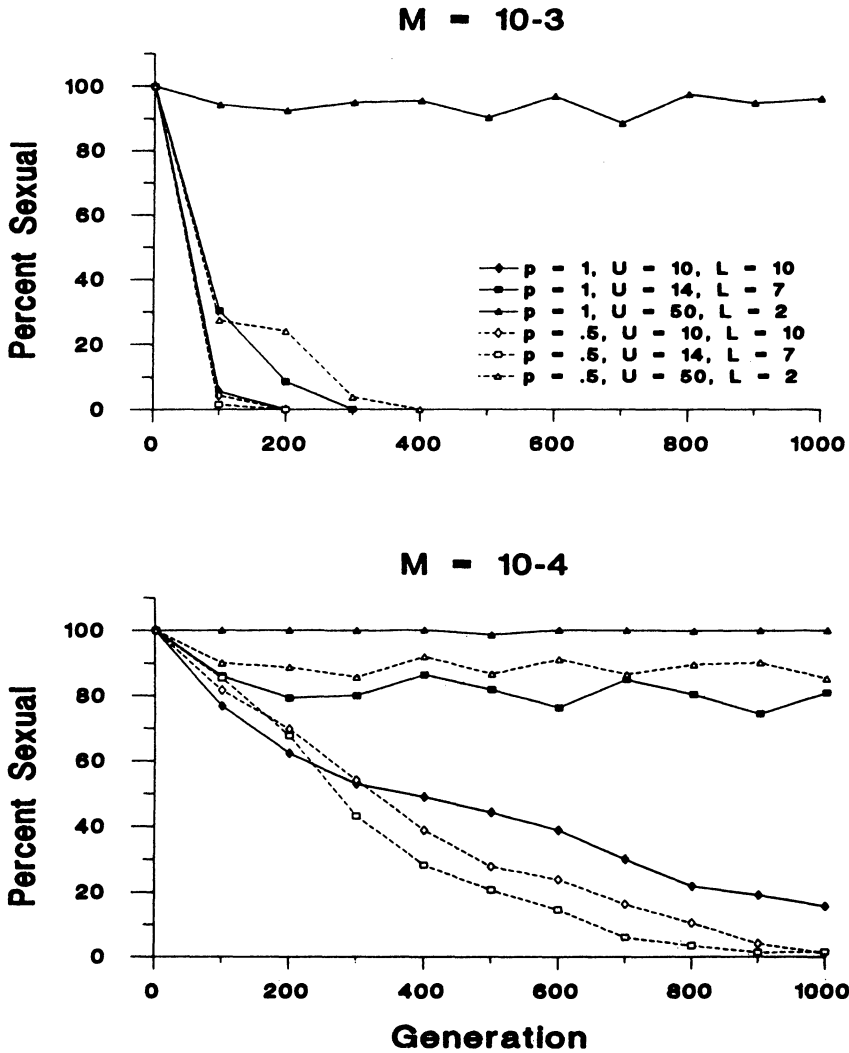


FIG. 6.—Persistence times of sexual populations in trials with temporally variable environments. All trials assumed uniform resource distributions. Two levels of asexual mutation rate are shown ($M = 1 \times 10^{-3}$ and 1×10^{-4}). Within-phenotype niche width, p , was set at 0 (filled symbols and solid lines) and 0.5 (open symbols and dashed lines). Resource variance, quantified by $[U, L]$ (see text), was set at $[10, 10]$, $[14, 7]$, and $[50, 2]$, which produced an expectation of resource extinction of $1/1,024$, $1/128$, and $1/4$ per resource per generation, respectively.

TABLE 3
AVERAGE GENETIC DIVERSITY PARAMETER, H , AS A FUNCTION OF TIME IN SIX EXAMPLE TRIALS

GENERATION	TRIALS											
	A		B		C		D		E		F	
	%	H	%	H	%	H	%	H	%	H	%	H
10	100	.50	100	.50	30	.46	88	.50	97	.50	98	.50
40	100	.50	100	.50	0	...	36	.35	91	.49	93	.49
70	100	.50	100	.50	0	...	12	.16	86	.49	91	.50
100	100	.50	100	.50	0	...	16	.16	83	.49	86	.49
400	100	.50	100	.50	0	...	0	...	32	.28	86	.49
700	100	.50	100	.50	0	...	0	...	8	.21	85	.50
1,000	100	.50	100	.49	0	...	0	...	0	...	81	.47

NOTE.—Ten replicates were run per trial, and the mean percent sexuals and genetic diversity index are shown. All six trials were run with uniform resources, $p = 0.0$, K (or mean K) = 50, and $N = 20$. The six trials were as follows: A, $M = 0$, K fixed; B, $M = 0$, K variable ($[U, L] = [14, 7]$); C, $M = 10^{-2}$, K fixed; D, $M = 10^{-3}$, K fixed; E, $M = 10^{-4}$, K fixed; and F, $M = 10^{-4}$, K variable ($[U, L] = [14, 7]$).

Genetic Diversity

The average genetic diversity, H (Nei 1975), was computed for the four loci in each enumerated generation. The results of six trials are shown in table 3. In all cases in which the sexual population remained large, there was no significant loss of alleles to random genetic drift, even in cases in which the resources fluctuated to zero (cases B and F; table 3). In trials in which the sexuals were replaced by asexual mutants, average genetic diversity would remain high ($H > 0.45$) until 50% or more of the total sexual population had been lost. Therefore, genetic drift in the sexual population did not play a major role in the dynamics of the system over the time frame studied.

DISCUSSION

Bell (1982), Case and Taper (1986), and Koella (1988) have shown that increased relative niche width can maintain sex in coarse- or fine-grained environments when sexuals compete with one or a few clones. Case and Taper (1986) demonstrated that the sexuals' niche width need only be 5%–20% wider than that of the combined asexuals' niche for sexuals to be competitively superior. These models stressed low within-phenotype niche width, large genetically determined between-genotype niche width, and resource competition for sexuality to persist.

None of the above models allowed the possibility of periodic clonal recruitment from the sexual population. However, natural clonal populations are typified by recurrent clonal formation, either through interspecific hybridization (e.g., fish [Schultz 1977; Turner 1982; Goddard et al. 1989], salamanders [Uzzell 1964; Lowcock et al. 1987], lizards [Lowe and Wright 1966; Uzzell and Darevsky 1975; Parker and Selander 1976; Dessauer and Cole 1989], and grasshoppers [Hewitt 1975]), through incomplete meiosis (e.g., moths [Harshman and Futuyma 1985]),

or through male transmission of meiosis-disrupting genes (e.g., cladocerans [Innes and Hebert 1988] and earthworms [Jaenike and Selander 1979]). The realistic assumption of recurrent clonal formation requires a reassessment of the interaction of sexuals and asexuals in heterogeneous environments. I examined three aspects of clonal/sexual interactions: (1) the persistence time of sexuals in temporally stable environments, (2) the pattern of clonal invasion, and (3) the conditions that allow sexual/clonal coexistence.

Sexual Persistence

The mutation rate, M , clearly had the greatest effect on sexual persistence times. With M as low as 10^{-5} , sexual persistence was as long as 10,000 generations (fig. 3). Increased sampling error also prolonged sexual persistence, because of the increased likelihood of random clonal extinction (Bell 1982). The rate of clonal formation in natural populations remains unclear (Quattro et al. 1991). If clonal mutants are generated by point mutations, M could be as low as 10^{-6} to 10^{-9} , allowing sexuals to persist for millions of generations in heterogeneous environments. Sexual persistence on these time scales might allow long-term disadvantages of asexuality to be manifested, such as Muller's ratchet (Muller 1964), segregational load (Kirkpatrick and Jenkins 1989), or reduced recombinational repair (Bernstein et al. 1987), which would erode the twofold reproductive advantage of clones. Extended persistence times also could facilitate establishment of frequency-dependent factors such as diseases or predators that focus on common genotypes (i.e., red queen process [Bell 1982]) or the accumulation of mutations with epistatic effects on fitness (Kondrashov 1982, 1984), which could reduce or eliminate the advantage of clones. Alternately, if clones are generated by processes other than point mutations, such as interspecific hybridization (Uzzell 1964; Lowe and Wright 1966; Hewitt 1975; Schultz 1977) or male transmission of meiosis-disrupting genes (Innes and Hebert 1988), M could be 10^{-2} to 10^{-4} or higher. Clonal formation at this rate would necessitate shorter-term processes, such as fluctuating resources (see below) to reduce clonal spread. Further studies addressing the rates of clonal formation in natural populations will help to clarify these alternatives and thus to evaluate the importance of "long-term" versus "short-term" advantages to sex.

Nonrandom Clonal Invasion

Periodic meiotic-suppressing mutants result in the "freezing" of multiple sexual genotypes. A natural assumption is that all genotypes should be equally likely to establish successful clones. This assumption was borne out in simulations with Gaussian resource distributions (table 1). However, in simulations with uniform resource distributions, a "centripetal" asexual invasion pattern was revealed, the result of the combination of meiotic processes and random mating. In every generation, sexual adults create a polygenic distribution of offspring through recombination, producing many individuals with mean phenotypes and fewer individuals with marginal phenotypes (Roughgarden 1972). Clones of any one phenotype must compete with a proportion of sexual offspring generated by adults of other phenotypes, which diminishes the clone's twofold reproductive advantage.

The extent of the relative reproductive loss is dependent on the "commonness" of the clone's phenotype relative to the sexuals' phenotypic distribution and the resource distribution. In uniform habitats, clones with central phenotypes will experience higher competition relative to clones with marginal phenotypes (fig. 5A, C). This increased competition will lead to a lower asexual equilibrium number and an increased likelihood of random asexual extinction for clones with central phenotypes. When the resource distribution more closely approximates the progeny distribution (Gaussian distribution; fig. 5B, D), competition is more uniform across resources and clonal extinction is less likely, leading to a random asexual invasion pattern.

If natural resources tend to be uniformly distributed, then the centripetal clonal invasion pattern described here could help to explain the predominance of clones in marginal habitats (Wright and Lowe 1968; Bell 1982; Lynch 1984; Moore 1984; Vrijenhoek 1984; Bierzychudek 1985). If marginal habitats are defined as those in which sexuals with appropriately adapted phenotypes are rarely produced and yet resources in marginal habitats are abundant, asexual mutants freezing uncommon or "marginal" phenotypes should prosper. We can predict that in environments with uniformly distributed resources, initially successful clones are those with marginal phenotypes, and only as the sexual population decreases in size should asexual mutants freezing the common or "central" phenotypes be successful invaders. However, organisms with overlapping generations will be better able to match their environment, thereby distorting the distribution of phenotypes away from the segregation kernel (Case and Taper 1986). Thus, the prediction that clones are more successful in freezing marginal phenotypes may be restricted to short-lived, semelparous organisms rather than long-lived, iteroparous ones.

Sexual/Clonal Coexistence

Previous models have clearly shown that sexuals can coexist with one or a few clones in heterogeneous environments (Bell 1982; Case and Taper 1986). Bell

(1982) noted that sexual persistence in populations with multiple clones requires processes that cause clonal extinctions. He outlines a hypothetical example in which eight clones are in competition with a sexual population and, through random clonal loss, sexuality is fixed at some undetermined future point (Bell 1982, fig. 2.13). Bell (1982) argued that sampling error and temporal changes in resource abundance could cause the random extinction of clones, but he never published a formal model of this situation.

In this study, the elimination of clones due to random sampling error and temporal resource fluctuations was compared. The results clearly show that sexual/clonal coexistence is more complicated than originally described by Bell

breadth. When both the probability of clonal formation and within-genotype niche breadth were low, the probability of resource extinction needed to be only about one out of 16,000 consumer generations for coexistence. Increased asexual mutation rates substantially increased the level of resource variation needed for coexistence (table 2). In fact, in trials with high mutation rates ($M = 10^{-2}$ to 10^{-3}), resource fluctuations needed to be so high that genetic diversity was eroded and sexual populations were slowly driven extinct. Increasing the within-individual niche width eliminated this loss of genetic diversity in the sexual populations. But increased p concomitantly decreased the probability of clonal extinction, which reduced the likelihood of sexual/clonal coexistence to high levels of resource fluctuations even at low asexual mutation frequencies. Thus, sexual/clonal coexistence in species with recurrent clonal formation appears to be confined to populations that rarely produce relatively specialized clones or to populations that rarely produce generalized clones in environments with large fluctuations in resources.

The assumption of a fixed carrying capacity in the current model may have given an advantage to the asexual lines (see Taper and Case 1985). If the carrying capacity for the nine resource types were responsive to consumer density, then resources that were under high demand would result in a lower carrying capacity (Case and Taper 1986). Under these circumstances, resources dominated by asexuals may have had lower carrying capacities, which might result in higher likelihood of extinction (Koella 1988), thereby extending the range of conditions under which the sexuals could persist. However, in a related model, the coexistence of sexual and clonal individuals was "hardly modified at all" by replacing the explicit resource dynamics by a constant carrying capacity (Case and Taper 1986, p. 372). Therefore, we might expect that the basic conclusions of the current model also would be little affected by the inclusion of responsive carrying capacities.

Factors other than temporal resource variation also can lead to clonal extinction. As mentioned above, high intrinsic rates of increase of asexual populations could cause clonal extinctions because of overexploitation of resources (Koella 1988). Also, long-term processes such as Muller's ratchet (Muller 1964), segregational load (Kirkpatrick and Jenkins 1989), or reduced recombinational repair (Bernstein et al. 1987) could lead to clonal extinction. Realistically, all of the above processes could combine to cause the extinction of both specialized and generalized clones and thus increase the conditions for sexual/clonal coexistence.

The short-term benefits of sex envisioned in the current model can be seen as complementary to long-term benefits of sex (Fisher 1930; Muller 1932; Crow and Kimura 1965; Maynard Smith 1968; Nunney 1989). In a recent model of the long-term advantages of sex, Nunney (1989) assumes that sexuality is costly to individuals such that, on an evolutionary time scale, "the displacement of sexual by asexual forms takes place fast enough to be considered instantaneous" (Nunney 1989, p. 247). The advantage of sex is assumed to be due to the avoidance of extinction. Sex is favored when differences in extinction rates between asexual and sexual species are greater than the rate of origin of asexual mutants in sexual populations. These conclusions are dependent on long-term, interspecific selection that favors sexual species with lower probabilities of clonal formation. Such

long-term processes can complement short-term extinctions, such as fluctuations in resource abundance, to maintain sex. Rather than assume the displacement of sexual by asexual forms is instantaneous, sexuals may be resistant to asexual invasion due to the short-term extinction processes discussed above. If clonal formation is high enough, short-term extinction processes will be unable to maintain sex, and long-term processes, such as the population extinctions proposed by Nunney, might then select for sexual populations with lower asexual mutation rates. Thus, sex may be maintained due to its resilience to short-term phenotypic extinction combined with its long-term avoidance of population extinction.

Future Research

Experimental tests of these evolutionary predictions are difficult to mount, and we must largely rely on comparative analyses of existing sexual/asexual complexes. Estimations of resource fluctuations, rates of clonal formation, short-term clonal persistence, and the relative values of within- and between-genotype niche widths are necessary to address short-term persistence of sexuals in populations with recurrent clonal formation. To address nonrandom clonal invasion, we need to estimate the sexuals' niche breadth, the relative proportion of sexuals with differing phenotypes, the abundance of the relevant resources, the number of coexisting clones, and their respective niche breadths. Measuring the proportion of sexuals with differing phenotypes is difficult and can only be accomplished by "probing" the sexual gene pool by freezing a number of genotypes in clonal or inbred lines (see Wetherington et al. 1987, 1989). From such information, we could define marginal and common sexual phenotypes and compare the success of clones freezing either phenotypic category. Also, by calculating the relative ages of the differing, naturally occurring clones, we could evaluate the expected positive correlation between clonal age and marginal phenotype.

Unfortunately, detailed ecological information is missing for most asexual/sexual complexes (see Vrijenhoek 1990). Although clonal diversity has been quantified in several organisms (Parker and Selander 1976; Vrijenhoek et al. 1977, 1978; Parker 1979; Jaenike et al. 1980, 1982; Hebert and Crease 1983), in many cases it is only beginning to be examined (Ellstrand and Roose 1987; Crease et al. 1989; Hebert et al. 1989; Honeycutt and Wilkinson 1989; Quattro et al. 1991). Future empirical studies addressing the short-term benefits of sexual reproduction should concentrate on sexual populations prone to clonal formation to specifically address sexual persistence in spatially and temporally fluctuating environments.

ACKNOWLEDGMENTS

I thank O. Gaggiotti, S. Handel, C. Lively, T. Meagher, P. Morin, P. Smouse, R. C. Vrijenhoek, and G. C. Williams for both valuable discussions and critical review of the manuscript and A. Kondrashov and three anonymous reviewers for their helpful suggestions. This work was funded in part by a National Science Foundation Doctoral Dissertation Support Grant (BSR-8815423) and by contract DE-AC0976SROO-819 between the U.S. Department of Energy and the University of Georgia.

LITERATURE CITED

- Bell, G. 1982. The masterpiece of nature: the evolution and genetics of sexuality. University of California Press, Berkeley and Los Angeles.
- Bernstein, H., F. A. Hopf, and R. E. Michod. 1987. The molecular basis for the evolution of sex. *Advanced Genetics* 24:323-370.
- Bierzchudek, P. 1985. Patterns in plant parthenogenesis. *Experientia (Basel)* 41:1255-1264.
- Case, T. J., and M. L. Taper. 1986. On the coexistence and coevolution of asexual and sexual competitors. *Evolution* 40:366-387.
- Crease, T. J., D. J. Stanton, and P. D. N. Hebert. 1989. Polyphyletic origins of asexuality in *Daphnia pulex*. II. Mitochondrial-DNA variation. *Evolution* 43:1016-1026.
- Crow, J. F., and M. Kimura. 1965. Evolution in sexual and asexual populations. *American Naturalist* 99:439-450.
- Dessauer, H. C., and C. J. Cole. 1989. Diversity between and within nominal forms of unisexual lizards. Pages 49-71 in R. M. Dawley and J. P. Bogart, eds. *Evolution and ecology of unisexual vertebrates*. New York State Museum, Albany.
- Ellstrand, N. C., and M. L. Roose. 1987. Patterns of genotypic diversity in clonal plant species. *American Journal of Botany* 74:123-131.
- Fisher, R. A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford.
- Ghiselin, M. T. 1974. The economy of nature and the evolution of sex. University of California Press, Berkeley.
- Goddard, K. A., R. M. Dawley, and T. E. Dowling. 1989. Origin and genetic relationships of diploid, triploid, and diploid-triploid mosaic biotypes in the *Phoxinus eos-neogaeus* unisexual complex. Pages 268-280 in R. M. Dawley and J. P. Bogart, eds. *Evolution and ecology of unisexual vertebrates*. New York State Museum, Albany.
- Harshman, L. G., and D. J. Futuyma. 1985. The origin and distribution of clonal diversity in *Alsophila pometaria* (Lepidoptera: Geometridae). *Evolution* 39:315-324.
- Hebert, P. D. N., and T. J. Crease. 1983. Clonal diversity in populations of *Daphnia pulex* reproducing by obligate parthenogenesis. *Heredity* 51:353-369.
- Hebert, P. D. N., R. D. Ward, and L. J. Weider. 1988. Clonal-diversity patterns and breeding-system variation in *Daphnia pulex*, an asexual-sexual complex. *Evolution* 42:147-159.
- Hebert, P. D. N., M. J. Beaton, S. S. Schwartz, and D. J. Stanton. 1989. Polyphyletic origins of asexuality in *Daphnia pulex*. I. Breeding-system variation and levels of clonal diversity. *Evolution* 43:1004-1015.
- Hewitt, G. M. 1975. A new hypothesis for the origin of the parthenogenetic grasshopper *Moraba virgo*. *Heredity* 34:117-136.
- Honeycutt, R. L., and P. Wilkinson. 1989. Electrophoretic variation in the parthenogenetic grasshopper *Warramaba virgo* and its sexual relatives. *Evolution* 43:1027-1044.
- Innes, D. J., and P. D. N. Hebert. 1988. The origin and genetic basis of obligate parthenogenesis in *Daphnia pulex*. *Evolution* 42:1024-1035.
- Jaenike, J., and R. K. Selander. 1979. Evolution and ecology of parthenogenesis in earthworms. *American Zoologist* 19:729-737.
- Jaenike, J., E. D. Parker, Jr., and R. K. Selander. 1980. Clonal niche structure in the parthenogenetic earthworm *Octolasion tyraeum*. *American Naturalist* 116:196-205.
- Jaenike, J., S. Ausubel, and D. A. Grimaldi. 1982. On the evolution of clonal diversity in parthenogenetic earthworms. *Pedobiologia* 23:304-310.
- Kirkpatrick, M., and C. D. Jenkins. 1989. Genetic segregation and the maintenance of sexual reproduction. *Nature (London)* 339:300-301.
- Koella, J. C. 1988. The tangled bank: the maintenance of sexual reproduction through competitive interactions. *Journal of Evolutionary Biology* 1:95-116.
- Kondrashov, A. S. 1982. Selection against harmful mutations in large sexual and asexual populations. *Genetical Research* 40:325-332.
- . 1984. Deleterious mutations as an evolutionary factor. I. The advantage of recombination. *Genetical Research* 44:199-217.
- Lowcock, L. A., L. E. Licht, and J. P. Bogart. 1987. Nomenclature in hybrid complexes of *Ambly-*

- stoma* (Urodela: Ambystomatidae): no case for the erection of hybrid "species." *Systematic Zoology* 36:328–336.
- Lowe, C. H., and J. W. Wright. 1966. Evolution of parthenogenetic species of *Cnemidophorus* (whiptail lizards) in western North America. *Journal of the Arizona Academy of Sciences* 4:81–87.
- Lynch, M. 1984. Destabilizing hybridization, general-purpose genotypes and geographic parthenogenesis. *Quarterly Review of Biology* 59:257–290.
- Maynard Smith, J. 1968. Evolution in sexual and asexual populations. *American Naturalist* 102:469–473.
- . 1976. A short term advantage for sex and recombination through sib-competition. *Journal of Theoretical Biology* 63:245–258.
- Michod, R. E., and B. R. Levin. 1988. *The evolution of sex: an examination of current ideas*. Sinauer, Sunderland, Mass.
- Moore, W. S. 1984. Evolutionary ecology of unisexual fishes. Pages 329–397 in B. J. Turner, ed. *Evolutionary genetics of fishes*. Plenum, New York.
- Muller, H. J. 1932. Some genetic aspects of sex. *American Naturalist* 66:118–138.
- . 1964. The relation of recombination to mutational advance. *Mutational Research* 1:2–9.
- Nei, M. 1975. *Molecular population genetics and evolution*. American Elsevier, New York.
- Nunney, L. 1989. The maintenance of sex by group selection. *Evolution* 43:245–257.
- Parker, E. D. 1979. Ecological implications of clonal diversity in parthenogenetic morphospecies. *American Zoologist* 19:753–762.
- Parker, E. D., and R. K. Selander. 1976. The organization of genetic diversity in the parthenogenetic lizard *Cnemidophorus tesselatus*. *Genetics* 84:791–805.
- Quattro, J. M., J. C. Avise, and R. C. Vrijenhoek. 1991. Molecular evidence for multiple origins of hybridogenetic fish clones (Poeciliidae: *Poeciliopsis*). *Genetics* 127:391–398.
- Roughgarden, J. 1972. Evolution of niche width. *American Naturalist* 106:683–718.
- Schultz, R. J. 1977. Evolution and ecology of unisexual fishes. *Evolutionary Biology* 10:277–331.
- Stearns, S. C. 1987. *The evolution of sex and its consequences*. Birkhauser, Basel.
- Taper, M. L., and T. J. Case. 1985. Quantitative genetic models for the coevolution of character displacement. *Ecology* 66:355–371.
- Turner, B. J. 1982. The evolutionary genetics of a unisexual fish, *Poecilia formosa*. Pages 265–306 in C. Barigozzi, ed. *Mechanisms of speciation*. Liss, New York.
- Uzzell, T. 1964. Relations of the diploid and triploid species of the *Ambystoma jeffersonianum* complex (Amphibia, Caudata). *Copeia* 1964:257–300.
- Uzzell, T., and I. S. Darevsky. 1975. Biochemical evidence for the hybrid origin of the parthenogenetic species of the *Lacerta saxicola* complex (Sauria, Lacertidae), with a discussion of some evolutionary and ecological implications. *Copeia* 1975:204–222.
- Vrijenhoek, R. C. 1979. Factors affecting clonal diversity and coexistence. *American Zoologist* 19:787–797.
- . 1984. Ecological differentiation among clones: the frozen niche-variation model. Pages 217–231 in K. Wohrman and V. Loschcke, eds. *Population biology and evolution*. Springer, Berlin.
- . 1990. Genetic diversity and the ecology of asexual populations. Pages 175–197 in K. Wohrman and V. Loschcke, eds. *Population biology*. Springer, Berlin.
- Vrijenhoek, R. C., R. A. Angus, and R. J. Schultz. 1977. Variation and heterozygosity in sexually vs. clonally reproducing populations of *Poeciliopsis*. *Evolution* 31:767–781.
- . 1978. Variation and clonal structure in a unisexual fish. *American Naturalist* 112:41–55.
- Wetherington, J. D., K. E. Kotora, and R. C. Vrijenhoek. 1987. A test of the spontaneous heterosis hypothesis for unisexual vertebrates. *Evolution* 41:721–731.
- Wetherington, J. D., S. C. Weeks, K. E. Kotora, and R. C. Vrijenhoek. 1989. Genotypic and environmental components of variation in growth and reproduction of fish hemiclones (*Poeciliopsis*: Poeciliidae). *Evolution* 43:635–645.
- White, M. J. D. 1978. *Modes of speciation*. W. H. Freeman, San Francisco.
- Wright, J. W., and C. H. Lowe. 1968. Weeds, polyploids, parthenogenesis, and the geographical and ecological distribution of all-female species of *Cnemidophorus*. *Copeia* 1968:128–138.