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STABLE TWO-ALLELE POLYMORPHISMS MAINTAINED BY FLUCTUATING FITNESSSES AND SEED BANKS: PROTECTING THE BLUES IN *LINANTHUS PARRYAE*

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Abstract.—Motivated by data demonstrating fluctuating relative and absolute fitnesses for white- versus blue-flowered morphs of the desert annual *Linanthus parryae*, we present conditions under which temporally fluctuating selection and fluctuating contributions to a persistent seed bank will maintain a stable single-locus polymorphism. In *L. parryae*, blue flower color is determined by a single dominant allele. To disentangle the underlying diversity-maintaining mechanism from the mathematical complications associated with departures from Hardy-Weinberg genotype frequencies and dominance, we successively analyze a haploid model, a diploid model with three distinguishable genotypes, and a diploid model with complete dominance. For each model, we present conditions for the maintenance of a stable polymorphism, then use a diffusion approximation to describe the long-term fluctuations associated with these polymorphisms. Our protected polymorphism analyses show that a genotype whose arithmetic and geometric mean relative fitnesses are both less than one can persist if its relative fitness exceeds one in years that produce the most offspring. This condition is met by data from a population of *L. parryae* whose white morph has higher fitness (seed set) only in years of relatively heavy rain fall. The data suggest that the observed polymorphism may be explained by fluctuating selection. However, the yearly variation in flower color frequencies cannot be fully explained by our simple models, which ignore age structure and possible selection in the seed bank. We address two additional questions—one mathematical, the other biological—concerning the applicability of diffusion approximations to intense selection and the applicability of long-term predictions to datasets spanning decades for populations with long-lived seed banks.

Key words.—Diffusion approximation, flower color polymorphism, fluctuating selection, Frank's distribution, seed bank.

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Through the seminal papers of Epling and Dobzhansky (1942) and Wright (1943a, b), the flower color polymorphism in the diminutive desert annual *Linanthus parryae* played a central role in shaping population genetic theory and opinions concerning the roles of natural selection, genetic drift, and migration in evolution. In their 1941 survey of 427 sampling locations in the Mojave Desert, California, Epling and Dobzhansky (1942) found a preponderance of monomorphic populations with most having white flowers. About 19% of their 1261 samples were polymorphic, and white flowers predominated in most of these. Wright (1943b; 1978, pp. 194–223) analyzed the spatial pattern of flower color frequencies and concluded that despite some evidence for directional selection favoring white, selection was generally negligible, and drift, migration and, possibly, mutation-selection balance determined allele frequencies in these populations. Wright argued that the effects of drift could explain the spatial pattern of polymorphic frequencies if effective local population sizes were on the order of 100 or less. However, after monitoring these same populations for another 15 years, Epling et al. (1960) found little change in local flower-color frequencies. Based on this constancy and experimental evidence for a long-lived seed bank, Epling et al. (1960) concluded that the importance of genetic drift had been overestimated and that “the frequencies of blue and white flowered plants are in the

long run the product of selection operating at an intensity we have been unable to measure.”

Schemske and Bierzychudek (2001) report more than a decade of fitness data that strongly support Epling et al.'s (1960) interpretation. Only a cursory summary of the data will be provided here to motivate our mathematical analyses. At two sites with monomorphic populations, Schemske and Bierzychudek (2001) performed transplant experiments that showed directional selection favoring the local morph. In an area that was polymorphic in 1941 and has remained polymorphic in recent surveys, they found fluctuating directional selection in seed production, with white-flowered plants out producing blue-flowered plants in wetter-than-average years and blue-flowered plants out producing whites in dryer-than-average years. In addition to the fluctuating relative fitnesses, they also found dramatic fluctuations in plant density and absolute seed production. In very dry years, no plants appeared; in dry years, there were five to 30 seeds per plant; while in years with high rainfall, individual plants produced hundreds of seeds. Simultaneously, plant densities varied more than 40-fold among years in which seeds were produced. Schemske and Bierzychudek's data show that selection contributes to the spatial pattern of flower-color frequencies. The question we address here is whether the observed temporal variation in absolute and relative fitnesses is sufficient to explain persistent local polymorphism without invoking migration between habitats in which selection favors the alternative morphs. The analysis is greatly simplified

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by the fact that the *Linanthus* flower color dimorphism is controlled by a diallelic locus with blue dominant to white (Epling et al. 1960; Wright 1978, pp. 194–195; P. Bierzychudek, unpubl. data).

Before addressing the data, we will present a mathematical analysis of conditions under which temporally fluctuating selection combined with fluctuating contributions to a seed bank can maintain variation at a diallelic locus. Dempster (1955) provided the first correct analysis of temporally fluctuating selection (reviewed in Gillespie 1991, sec. 4.7). He analyzed a haploid model and demonstrated that fluctuating selection led to the fixation of the genotype with the highest geometric mean fitness. Haldane and Jayakar (1963) showed that fluctuating selection on diploids could maintain polymorphisms. Assuming discrete generations and complete dominance, they found that a stable polymorphism would be maintained if the relative fitness of the recessive genotype, denoted w , satisfied two conditions: Its arithmetic mean, $E(w)$, must exceed one; but its geometric mean, $\exp\{E[\ln(w)]\}$, must be less than one. Gillespie has developed the most extensive body of theory delimiting conditions under which fluctuating selection will maintain genetic variation (see Gillespie 1991), but he has not specifically addressed the effects of overlapping generations.

Templeton and Levin (1979) analyzed temporally fluctuating selection on plants with seed banks. They used numerical simulations of complex models involving age structure and age-dependent selection both during dormancy and after germination to demonstrate that seed banks facilitate the maintenance of polymorphism. Subsequently, considerable analytical progress has been made in understanding stochastic age-structured models (e.g., Tuljapurkar 1990; Orzack 1993). However, we cannot apply these models because the necessary age-specific data on seed survival and germination are not available. The simple models we analyze below are much closer to the ecological lottery-competition models investigated by Chesson and his collaborators (e.g., Chesson and Warner 1981; Hatfield and Chesson 1989; Chesson 1994). They have shown that coexistence of competing species is facilitated by the combined effects of overlapping generations and fluctuating conditions that favor different competitors in different breeding seasons. Similar analyses have been adapted to the maintenance of genetic variation for multiple alleles and loci by Ellner and his collaborators (e.g., Ellner and Hairston 1994; Ellner and Sasaki 1996; Ellner et al. 1999). Seger and Brockmann (1987) and Hedrick (1995) demonstrated the polymorphism-preserving role of seed banks with simple one-locus, two-allele models that ignore season-to-season variation in seed set. Our slightly more complex models, which include variation in productivity, analytically capture a key insight of Templeton and Levin's (1979) simulations—the importance of covariance between seed production and relative fitnesses. Our attempt at understanding the *L. parryae* polymorphism in terms of a specific model complements Subramaniam and Rausher's (2000) experimental approach to demonstrating that balancing selection maintains the flower-color polymorphism in the morning glory, *Ipomoea purpurea*.

Our goal is to make empirically useful qualitative and

quantitative predictions in terms of estimable parameters rather than capturing all aspects of the biology. We first develop a sequence of simple models that illustrate the key ideas. We compare exact conditions for the maintenance of stable polymorphisms with simpler conditions derived from diffusion approximations. We use the diffusions to characterize the polymorphisms and test the accuracy of their predictions for the mean and standard deviation of allele frequencies against numerical simulations. Finally, we apply the theoretical results to some *L. parryae* data from Schemske and Bierzychudek (2001). Readers uninterested in the mathematical details should skip to the section analyzing the *Linanthus* data after reading the introductory descriptions of the models.

MODELS AND ANALYSES

Model

Throughout we will consider a single, diallelic autosomal locus in an annual, with alleles denoted A_1 and A_2 . The long-term fate of these alleles will be determined by their persistence in the seed bank. For simplicity, we will assume that selection acts only on adult fecundity. Epling et al. (1960) and Wright (1978, pp. 194–223) report that although germination rates vary dramatically across years, genotype-specific differences in germination rates seemed negligible. To study the properties of the seed bank, they removed flowering plants before seed-set for several years in experimental plots. As estimated by Wright (1978, pp. 196–197), seedling density declined by only about 50% after 7 years, indicating a long-lived seed bank. Although Wright (1978, p. 197) concluded that there was no apparent viability selection among the dormant seeds, our χ^2 test of homogeneity from the three site B samples reported in figure 10 of Epling et al. (1960) shows statistically significant differences among years in flower-color frequencies, despite the fact that the samples in the first and last years are not significantly different. Thus, Wright's conclusion of no *consistent* differential viability seems valid, but the data also suggest genotype- and/or age-specific year-to-year variation in germination and/or seedling survival rates. Given that we have no data on these components of fitness, we ignore them in our mathematical analyses, but reconsider them below.

Given the available data, we will not partition male and female reproductive functions and will assume that the key fitness differences can be captured by estimating the average number of seeds produced by each phenotype. We assume that viability of seeds and germination rates are independent of genotype at this locus and that all seeds in the seed bank are equivalent, independent of age. These simplifying assumptions are not likely to be valid in the field. Our hope is that the effects of the large observed differences in absolute and relative seed set dominate the smaller effects associated with fitness components that have not been estimated. These assumptions are testable, as demonstrated below, and our model can be generalized toward Templeton and Levin's (1979) more realistic treatment as additional data become available.

Let p_t denote the frequency of allele A_1 in the seed bank just before germination in year t . Because there is no effect

of genotype on germination, p_t is also the allele frequency among new seedlings. Let p'_t denote the frequency of A_1 among seeds produced in year t . We assume that just before germination in year $t + 1$, a fraction a_t of all seeds in the seed bank was produced by adult plants in year t . Thus, the recursion for p_t is

$$p_{t+1} = (1 - a_t)p_t + a_t p'_t. \tag{1}$$

Favorable conditions will be associated with relatively large values of a_t , corresponding to greater input into the seed bank. Our frequency-based model ignores the ecological complexities that govern the absolute size of the seed bank.

Analyzing the diploid model relevant to *Linanthus* is complicated by dominance and the fact that the seed bank consists of a mixture of genotypes produced by selection in different generations. The mixture produces a temporal Wahlund effect (Christiansen 1988), so that the seedling genotype frequencies will generally not follow Hardy-Weinberg proportions, and the allele frequency, p_t , is insufficient to describe the exact evolutionary dynamics. Because these mathematical complications obscure the forces maintaining variation, we analyze in turn three different genetic models: (1) haploid selection; (2) diploid selection with heterozygotes having intermediate fitness; and (3) diploid selection with complete dominance. We focus on deriving analytical conditions for the maintenance of stable polymorphisms, then present diffusion approximations to describe the properties of these polymorphisms. Our general conclusions relate to the maintenance of single-locus polymorphisms in any population with discrete breeding seasons and overlapping generations.

Selection on Haploids

For haploids (or diploids with complete selfing), the evolutionary dynamics are completely characterized by p_t . Letting $w_{1,t}$ ($w_{2,t}$) denote the fitness of genotype A_1 (A_2) in generation t , we have

$$p'_t = \frac{p_t w_{1,t}}{p_t w_{1,t} + (1 - p_t) w_{2,t}} \tag{2}$$

in equation (1). We seek conditions for stochastic protected polymorphism (Prout 1968), that is, conditions that preclude either allele frequency from converging to zero over time. We will not provide a rigorous mathematical analysis; however, it can be shown (cf. Karlin and Liberman 1975) that the following heuristic argument produces the correct polymorphism conditions. When A_1 is extremely rare, that is, $p_t \cong 0$, the dynamics of recursion (1) can be approximated by

$$p_{t+1} = (1 - a_t)p_t + a_t p_t \frac{w_{1,t}}{w_{2,t}} = p_t \left(1 - a_t + a_t \frac{w_{1,t}}{w_{2,t}} \right). \tag{3}$$

This corresponds to the standard recursion for population growth in a random environment, so the condition for p_t to stay away from zero in the long run (i.e., $P[p_t \rightarrow 0 \text{ as } t \rightarrow \infty] = 0$) is simply

$$E \ln \left[1 + a_t \left(\frac{w_{1,t}}{w_{2,t}} - 1 \right) \right] > 0, \tag{4}$$

where E denotes mathematical expectation over the distribution of the random vector $(a_t, w_{1,t}, w_{2,t})$ (for a discussion

of such models and their diffusion approximations, see Turelli 1977). Essentially the same condition was derived by Chesson and Warner (1981), who demonstrated the potential for environmental variation to promote the coexistence of competing species (compare eqs. 3 and 12 of Chesson and Warner 1981). The case with a_t constant was discussed by Seger and Brockmann (1987). Because $\ln(1 + x)$ is a concave function (i.e., has a negative second derivative), Jensen's inequality implies that

$$E \ln \left[1 + a_t \left(\frac{w_{1,t}}{w_{2,t}} - 1 \right) \right] \leq \ln \left\{ 1 + E \left[a_t \left(\frac{w_{1,t}}{w_{2,t}} - 1 \right) \right] \right\}, \tag{5}$$

where equality holds only if there is no variation. It follows from inequalities (4) and (5) that a necessary condition for the protection of A_1 is

$$E \left[a_t \left(\frac{w_{1,t}}{w_{2,t}} - 1 \right) \right] > 0. \tag{6}$$

To clarify the role of the fluctuating contributions to the seed bank, let $a_t = az_t$, where $a = E(a_t)$ measures the average fraction of each generation's pregermination seed bank that consists of seeds produced the previous year. We assume that $0 < a < 1$. The random variable z_t describes the fluctuations in seed production, by definition it satisfies $E(z_t) = 1$. With this notation, (6) reduces to

$$E \left(z_t \frac{w_{1,t}}{w_{2,t}} \right) = E \left(\frac{w_{1,t}}{w_{2,t}} \right) + \text{Cov} \left(z_t, \frac{w_{1,t}}{w_{2,t}} \right) > 1. \tag{7}$$

Condition (7) requires that the weighted relative fitness of A_1 exceed one, where the weightings involve the fluctuating contributions to the seed bank. The weighting implies that A_1 can persist even if it performs relatively poorly on average (so that $E(w_{1,t}/w_{2,t}) < 1$), as long as this is offset by performing sufficiently better than A_2 in years that contribute most to the seed bank (so that $\text{Cov}[z_t, w_{1,t}/w_{2,t}]$ is sufficiently large). An empirical example is provided by the *L. parryae* data discussed below.

The condition analogous to (4) for the protection of A_2 (i.e., $P[p_t \rightarrow 1 \text{ as } t \rightarrow \infty] = 0$) is

$$E \ln \left[1 + a_t \left(\frac{w_{2,t}}{w_{1,t}} - 1 \right) \right] > 0. \tag{8}$$

As above, a necessary condition for A_2 to persist is

$$E \left(z_t \frac{w_{2,t}}{w_{1,t}} \right) = E \left(\frac{w_{2,t}}{w_{1,t}} \right) + \text{Cov} \left(z_t, \frac{w_{2,t}}{w_{1,t}} \right) > 1. \tag{9}$$

When both conditions (4) and (8) are met, we have a protected polymorphism; it is necessary, but not sufficient, to have both (7) and (9) satisfied.

As a approaches zero, conditions (7) and (9) do suffice for the maintenance of protected polymorphism (Chesson and Warner 1981). When there is no correlation between a_t and the relative fitnesses, for instance when a_t is constant, these necessary conditions reduce to

$$E \left(\frac{w_{1,t}}{w_{2,t}} \right) > 1 \quad \text{and} \tag{10a}$$

$$E \left(\frac{w_{2,t}}{w_{1,t}} \right) > 1. \tag{10b}$$

As illustrated below, these conditions, which may seem mutually exclusive, are both satisfied whenever the differences between the arithmetic means of the two relative fitnesses are small relative to their variances.

With no seed bank, that is, with $a_t \equiv 1$, no protected polymorphism is possible under this model. As shown by Dempster (1955), the population becomes monomorphic for the allele with the higher geometric mean fitness, that is, the higher value of $E[\ln(w_{i,t})]$. As $a = E(a_t)$ decreases, the range of parameters producing a protected polymorphism increases to the region defined by (10a, b). To quantify this effect simply, we will assume that the fitnesses follow lognormal distributions, so that $\ln(w_{1,t})$ and $\ln(w_{2,t})$ follow normal distributions with means μ_1 and μ_2 , variances σ_1^2 and σ_2^2 , and correlation ρ . The variability of the relative fitnesses can be expressed in terms of $\sigma^2 = \text{Var}[\ln(w_{1,t}/w_{2,t})] = \sigma_1^2 + \sigma_2^2 - 2\rho\sigma_1\sigma_2$. The difference in the geometric mean fitnesses of the genotypes can be quantified by $|\mu_1 - \mu_2| = |E[\ln(w_{1,t}/w_{2,t})]|$. The lognormal assumptions imply that $w_{1,t}/w_{2,t}$ also has a lognormal distribution with mean $\exp[\frac{\mu_1 - \mu_2}{2} + (\sigma^2/2)]$ and coefficient of variation (CV) $\sqrt{\exp(\sigma^2) - 1}$. Thus, the necessary conditions (10a, b) are satisfied whenever

$$\text{Var}[\ln(w_{1,t}/w_{2,t})] > 2|E[\ln(w_{1,t}/w_{2,t})]|, \quad (11)$$

which implies that differences in the geometric means must be compensated by sufficient fluctuation in the relative fitnesses (cf. Chesson and Warner 1981, fig. 1). The expected values in conditions (4) and (8) can be obtained numerically using Mathematica (Wolfram 1996). These exact results, which require specifying the full distributions of all of the random variables, will be numerically compared below to the results of a diffusion approximation, which depends only on means, variances and covariances.

In general, superimposing fluctuations in a_t that are independent of the relative fitnesses will make the protected polymorphism conditions slightly more restrictive. To see this, use the Jensen's inequality argument from (5), after conditioning on the values of $w_{1,t}$ and $w_{2,t}$, to obtain

$$E \ln \left[1 + a_t \left(\frac{w_{1,t}}{w_{2,t}} - 1 \right) \right] < E \ln \left[1 + E(a_t) \left(\frac{w_{1,t}}{w_{2,t}} - 1 \right) \right], \quad (12)$$

whenever a_t varies. This small effect will be quantified below along with the much larger effects of fluctuations in a_t that are correlated with $w_{1,t}/w_{2,t}$.

Diffusion approximation and numerical results

The analyses above provide conditions for protected polymorphism. But for many purposes, we will want to know properties of these polymorphisms, such as the long-term mean and variance of the allele frequencies. These are very difficult to obtain analytically for the discrete-time, nonlinear stochastic process defined by (1) and (2), but they can be approximated using diffusion theory. This process involves approximating a discrete-time process by a continuous-time process and is justified by assuming weak selection. As discussed below, this requires approximating the stochastic selection process and leads to conditions for polymorphism that generally differ somewhat from the exact conditions derived from the original model. There is no general theory to bound

the accuracy of these predictions, so numerical simulations are needed to evaluate their usefulness. For simplicity, we restrict our analyses by assuming that the random variables ($a_t, w_{1,t}, w_{2,t}$) are independent from generation to generation, so that (1) is a Markov process (cf. Gillespie 1991, ch. 4). Wright (1948) pioneered diffusion approximations of fluctuating selection. However, mathematical errors led both Wright (1948) and Kimura (1954) to conclude mistakenly that fluctuating selection could not maintain genetic variation. Their analyses were corrected by Gillespie (1973, 1974) and extended to diploids by Levikson and Karlin (1975; for treatment of an ecological analog of eq. 1, see Hatfield and Chesson 1989).

Diffusion approximations assume that selection is relatively weak and the stochastic fluctuations in the parameters are relatively small (see the Appendix for an elaboration). We present a new approach for applying these weak-selection, small-noise approximations to biological circumstances in which selection is strong and stochastic fluctuations extreme then explore the range of parameter values for which the approximations are informative. The diffusion approximation characterizes the model's behavior by the infinitesimal mean, denoted $m(p)$, and the infinitesimal variance, denoted $v(p)$, which approximate $E(\Delta p_t | p_t = p)$ and $\text{Var}(\Delta p_t | p_t = p)$, respectively (Karlin and Taylor 1981, ch. 15, especially pp. 184–188). The Appendix shows that

$$m(p) = ap(1-p) \left[\gamma + C + \sigma^2 \left(\frac{1}{2} - p \right) \right] \quad \text{and} \quad (13a)$$

$$v(p) = a^2 \sigma^2 [p(1-p)]^2, \quad (13b)$$

where $\gamma = \mu - \frac{1}{2}\sigma^2$, μ denotes the average (arithmetic mean) intensity of selection in favor of A_1 , σ^2 denotes the variance in relative fitness, and C denotes the covariance between z_t and the relative fitness of A_1 . Note that $\sigma_z^2 = \text{Var}(z_t) = [\text{CV}(a_t)]^2$ does not enter these expressions, reflecting the fact that to this order of approximation, variation in z_t contributes to the allele frequency evolution only when it covaries with the relative fitnesses (i.e., through the term C in eq. 13a). Gillespie (1991, ch. 4) discusses this same diffusion as his ‘‘c-haploid model,’’ including the consequences of autocorrelation.

When diffusion approximations are applied to discrete-time models in which the weak-selection, small-noise assumptions are not satisfied, there is a fundamental ambiguity in identifying the diffusion parameters with the moments of the random variables from the discrete-time model. For simple selection models like (1), we propose resolving this ambiguity with the following consistency criterion: the parameters must be chosen so that the resulting conditions for protected polymorphism and the moments of the allele frequency distribution are independent of whether we quantify selection by examining the relative fitnesses $w_{1,t}/w_{2,t}$ or $w_{2,t}/w_{1,t}$. Because this arbitrary choice for normalizing fitnesses does not affect the actual dynamics, a consistent diffusion approximation must be invariant to these alternative normalizations. This consistency criterion leads to

$$\gamma = E \left[\ln \left(\frac{w_{1,t}}{w_{2,t}} \right) \right], \tag{14a}$$

$$\sigma^2 = \text{Var} \left[\ln \left(\frac{w_{1,t}}{w_{2,t}} \right) \right], \text{ and} \tag{14b}$$

$$C = \text{Cov} \left[z_t, \ln \left(\frac{w_{1,t}}{w_{2,t}} \right) \right] \tag{14c}$$

(see the Appendix for details).

The diffusion process corresponding to (13) possesses a nontrivial, stationary distribution, corresponding to protected polymorphism, if and only if

$$|\gamma + C| < \frac{(1 - a)\sigma^2}{2} \tag{15}$$

(Karlin and Taylor 1981, pp. 220–221). When $\gamma + C > \frac{1}{2}(1 - a)\sigma^2$, A_1 spreads to fixation; whereas when $\gamma + C < -\frac{1}{2}(1 - a)\sigma^2$, A_2 spreads to fixation. Note that when $a_t \equiv 1$ for all t , corresponding to haploid selection with no seed bank, the protected polymorphism condition (15) cannot be satisfied. In this case, the approximation exactly reproduces Dempster's (1955) conclusion from the discrete-time model: A_1 spreads to fixation with probability one if and only if its geometric mean fitness exceeds that of A_2 , that is, $\gamma = E[\ln(w_{1,t}/w_{2,t})] > 0$.

Condition (15) makes several predictions. First note that if $C = 0$, implying that variation in contributions to the seed bank is uncorrelated with variation in relative fitnesses (i.e., neither allele is systematically favored in good years), variation in z_t does not affect the conditions for protected polymorphism. Second, note that γ and C enter (15) only as a sum. Thus, if allele A_1 has higher relative fitness in good years, this effectively raises its geometric mean relative fitness from $\gamma = E[\ln(w_{1,t}/w_{2,t})]$ to $E[\ln(w_{1,t}/w_{2,t})] + \text{Cov}[z_t, \ln(w_{1,t}/w_{2,t})]$. Third, for $a < 1$, condition (15) predicts that the minimum variance necessary to produce a protected polymorphism increases linearly with $|\gamma + C|$. Fourth, (15) predicts that this minimum variance is proportional to $1/(1 - a)$.

Figure 1 examines the third and fourth predictions. This figure compares the approximate protected polymorphism condition (15) to numerical results obtained from the exact conditions (4) and (8) assuming that a_t is constant and $w_{1,t}/w_{2,t}$ follows a lognormal distribution. The lines in Figure 1, corresponding to constant values of a , provide the minimum values of $\text{Var}[\ln(w_{1,t}/w_{2,t})]$ necessary to achieve a protected polymorphism for specified values of $|E[\ln(w_{1,t}/w_{2,t})]|$ (cf. fig. 1 of Chesson and Warner 1981; fig. 1 of Seger and Brockmann 1987; and fig. 1 of Hatfield and Chesson 1989). The results support the prediction that the minimum $\text{Var}[\ln(w_{1,t}/w_{2,t})]$ increases approximately linearly with $|E[\ln(w_{1,t}/w_{2,t})]|$. To appreciate the range of parameters explored, note that when $E[\ln(w_{1,t}/w_{2,t})] = 1.0$ (or 0.5), the geometric mean fitness of A_1 (i.e., $\exp\{E[\ln(w_{1,t})]\}$) exceeds that of A_2 by a factor of 2.72 (or 1.65). Not surprisingly, extreme levels of variation are needed to compensate for such large fitness differences. It is surprising, however, that our consistent diffusion approximation remains so accurate for such extreme levels of selection and variation. As predicted from (15), as

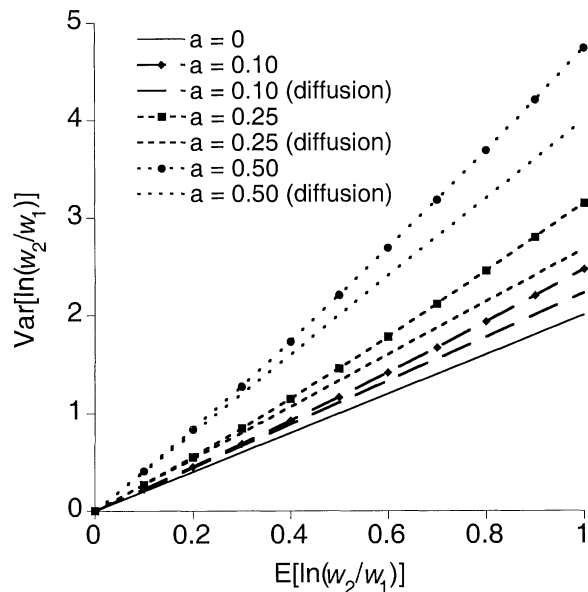


FIG. 1. Conditions for haploid protected polymorphisms with log-normally distributed fitnesses. The symbols indicate numerical approximations for the minimum variance in log relative fitnesses, $\text{Var}[\ln(w_{2,t}/w_{1,t})]$, necessary to produce a protected polymorphism despite a geometric mean fitness disadvantage for allele A_1 , as quantified by $E[\ln(w_{2,t}/w_{1,t})] > 0$. The lines are interpolations of the numerical values, except for the line corresponding to $a \rightarrow 0$, which is given by (11). The predictions from (15) are always within 16% of the numerically derived values, they remain within 9% for $|E[\ln(w_{1,t}/w_{2,t})]| \leq 0.5$. See the text for additional details.

a decreases, corresponding to a longer-lived seed bank, less variation in the relative fitnesses is needed to compensate for a given geometric mean fitness disadvantage. The ratio of the slopes of the best-fit linear regressions (forced through the origin) to the numerically obtained minimum values of $\text{Var}[\ln(w_{1,t}/w_{2,t})]$ with $a = 0.1$ versus $a = 0.5$ is 1.91, whereas (15) predicts a ratio of 1.8. Once a is as low as 0.1, the minimum variance is closely approximated by the necessary condition (11), corresponding to $a \rightarrow 0$.

The effect of varying a_t was quantified by assuming that z_t has a log-normal distribution truncated above at $1/a$ (so that $0 < a_t < 1$), whose moments were chosen so that $E(z_t) = 1$ and $\text{CV}(a_t)$ was equal to a specified value. The minimum value of $\text{Var}[\ln(w_{1,t}/w_{2,t})]$ consistent with maintaining a protected polymorphism was determined numerically from (4) and (8). For $\text{CV}(a_t) \leq 0.3$, the effect of variation in a_t is generally too small to display on the scale of Figure 1. Using $a = 0.25$ with $0.1 \leq E[\ln(w_{2,t}/w_{1,t})] \leq 1$, the relative increase in the critical value of $\text{Var}[\ln(w_{1,t}/w_{2,t})]$ was less than 1% for $\text{CV}(a_t) = 0.1$ versus $\text{CV}(a_t) = 0$, less than 2% for $\text{CV}(a_t) = 0.2$, and less than 3% for $\text{CV}(a_t) = 0.3$.

Figure 2 examines the predicted effects of $\text{Cov}[z_t, \ln(w_{1,t}/w_{2,t})]$. As expected, variation in a_t has a much larger effect when it systematically favors one of the alleles, example, when $\text{Cov}[z_t, \ln(w_{1,t}/w_{2,t})] > 0$, so that A_1 tends to have a higher relative fitness in years that make greater contributions to the seed bank. This positive covariance lowers the minimum variance in relative fitnesses needed to protect A_1 from loss when it has a geometric mean fitness disadvantage (i.e.,

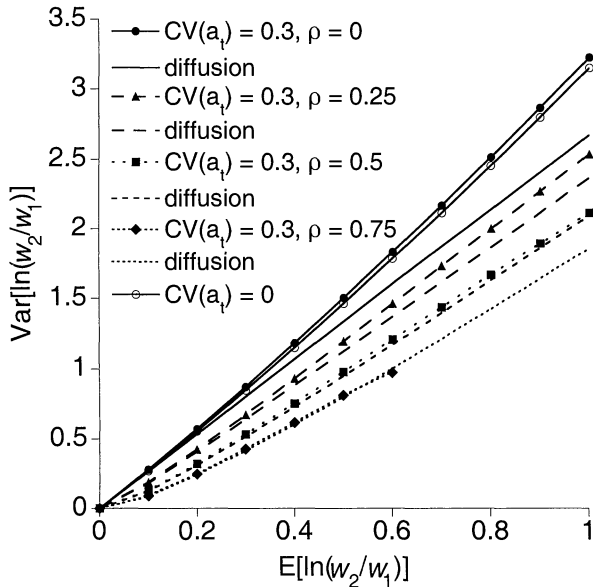


FIG. 2. Conditions for haploid protected polymorphisms with log-normally distributed fitnesses when the relative fitnesses are correlated with the inputs to the seed bank. As in Figure 1, the symbols indicate numerical approximations for the minimum variance in log relative fitnesses, $\text{Var}[\ln(w_{2,t}/w_{1,t})]$, necessary to produce a protected polymorphism despite a geometric mean fitness disadvantage for allele A_1 . For all of these calculations, $E(a_t) = 0.25$. ρ denotes the correlation between z_t , which describes the fluctuating contributions to the seed bank, and $\ln(w_{1,t}/w_{2,t})$, the relative fitness of A_1 . See the text for additional details.

$E[\ln(w_{1,t}/w_{2,t})] < 0$). This effect can be quantified by assuming that $(w_{1,t}/w_{2,t})$ and z_t have correlated log-normal distributions, with z_t truncated above at $1/a$. (Lognormality constrains the correlation between z_t and $\ln[w_{1,t}/w_{2,t}]$, details will be provided on request.) Figure 2 shows that even moderate positive correlations can significantly lower the variance needed to compensate for a geometric mean fitness disadvantage.

When condition (15) is satisfied, the stationary distribution, $\phi(p)$, which describes the long-term distribution of the frequency of A_1 , is

$$\phi(p) = \frac{\Gamma(b_1 + b_2)}{\Gamma(b_1)\Gamma(b_2)} p^{b_1-1}(1-p)^{b_2-1}, \quad (16a)$$

with

$$b_1 = \frac{2(\gamma + C) + (1-a)\sigma^2}{a\sigma^2} \quad \text{and} \quad (16b)$$

$$b_2 = \frac{-2(\gamma + C) + (1-a)\sigma^2}{a\sigma^2}. \quad (16c)$$

(see Karlin and Taylor 1981, pp. 220–221; Turelli 1981). This is a beta distribution with mean and standard deviation

$$E(p) = \frac{1}{2} + \frac{\gamma + C}{\sigma^2(1-a)} \quad \text{and} \quad (17a)$$

$$SD(p) = \frac{a}{4(2-a)} \left[1 - \left(\frac{2(\gamma + C)}{\sigma(1-a)} \right)^2 \right]. \quad (17b)$$

Note that $E(p) \rightarrow 1/2$ as σ^2 increases, displaying the poly-

morphism-promoting role of variation in relative fitnesses. The expression for $SD(p)$ shows that even when genetic variation is maintained by extreme fluctuations in fitness, allele frequencies will not fluctuate wildly if a is small, corresponding to prolonged dormancy in the seed bank.

The accuracy of the diffusion predictions concerning protected polymorphism was tested with replicated Monte Carlo simulations of the discrete-time model. As in our analysis of protected polymorphism, we assumed a log-normal distribution for $w_{1,t}/w_{2,t}$ with relative fitnesses independent across generations. Sample outcomes are presented in Figures 3 and 4. One hundred replicate simulations were performed for each parameter combination. Each simulation began at the expected allele frequency predicted by (17). After 500 generations, means and SDs were calculated from the allele frequencies generated over the next 10,000 generations. The values reported in Figures 3 and 4 for the means and SDs are averages of the means and SDs obtained from 100 replicates.

The two panels in Figure 3 compare the predictions from (17) to Monte Carlo results. For the parameter values used, the diffusion-based criterion (15) predicts a stable polymorphism for $|E[\ln(w_{1,t}/w_{2,t})]| < 0.267$; whereas the exact invasion analysis, (4) and (8), requires $|E[\ln(w_{1,t}/w_{2,t})]| < 0.272$. Given the close agreement of these bounds and the fact that the average allele frequency must increase from zero to one between the lower and upper bounds, the agreement between the predicted and observed means in Figure 3A may seem unremarkable. There is no comparable constraint, however, on the SDs displayed in Figure 3B, which show a similar level of agreement between the predicted and observed values. The two panels in Figure 4 compare the values predicted by (17) to Monte Carlo results as $\sigma^2 = \text{Var}[\ln(w_{1,t}/w_{2,t})]$ increases. As predicted, the average allele frequency converges toward $1/2$.

Selection on Diploids: Incomplete Dominance

The existence of a seed bank complicates the protected polymorphism analysis, because the allele frequency p_t no longer suffices to describe the composition of the seed bank. Even when adults mate randomly, so that the newly produced seeds follow Hardy-Weinberg proportions, fluctuating allele frequencies with $a_t < 1$ will generate a departure from Hardy-Weinberg proportions among seedlings (Christiansen 1988). A complete description of the evolutionary dynamics requires following genotype frequencies. Let $f(A_i A_j)_t$ denote the frequency of seeds of genotype $A_i A_j$ in the seed bank, just before germination in year t . We assume that the seed production of an adult is proportional to both its rate of pollen export and ovule production. We also assume random mating. With these assumptions, the combined effects of viability and fecundity differences among genotypes can be summarized by viability-analogous fitnesses (Bodmer 1965), denoted $w_{ij,t}$. The effective frequency of $A_i A_j$ adults in generation t is

$$f(A_i A_j)'_t = \frac{f(A_i A_j)w_{ij,t}}{\bar{w}_t}, \quad (18)$$

with $\bar{w}_t = f(A_1 A_1)w_{11,t} + f(A_1 A_2)w_{12,t} + f(A_2 A_2)w_{22,t}$. The

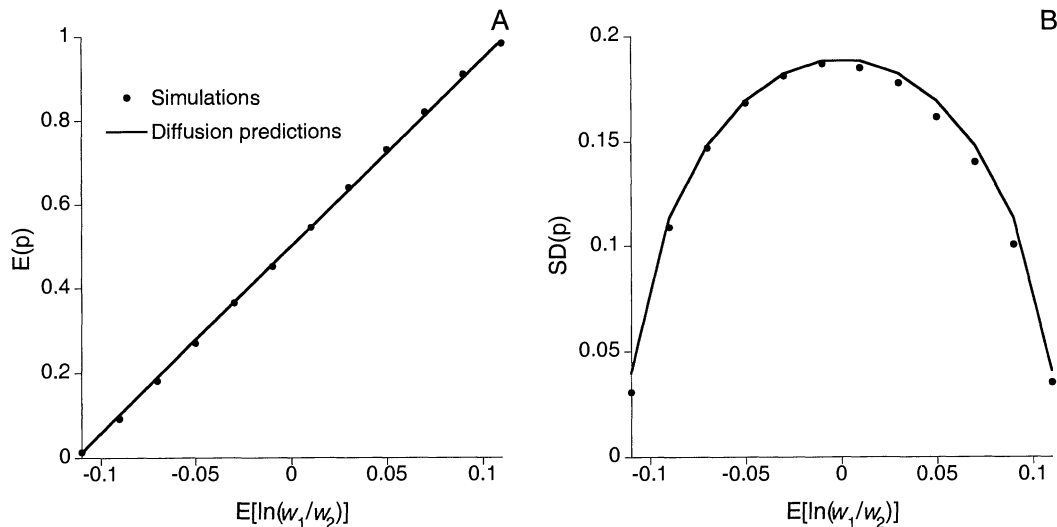


FIG. 3. Comparison of Monte Carlo results (dots) with the diffusion predictions (solid curve) for the mean (panel A) and the standard deviation (SD, panel B) of allele frequencies under haploid selection. The calculations assume that $a_t \equiv 0.25$ and $\sigma^2 = \text{Var}[\ln(w_{1,t}/w_{2,t})] = 0.3$, whereas $\gamma = E[\ln(w_{1,t}/w_{2,t})]$ ranges from -0.11 to 0.11 . Standard errors for the estimates were obtained from the 100 independent replicates, but were too small to display in the figures—the maximum value was 0.0028 for the estimates of $E(p)$ and 0.0025 for the estimates of $SD(p)$.

seeds produced by these adults follow Hardy-Weinberg proportions with allele frequency

$$f(A_1) \equiv p'_t = f(A_1A_1)'_t + \frac{1}{2}f(A_1A_2)'_t. \quad (19)$$

Thus, in the next generation, the genotype frequencies in the seed bank are given by

$$f(A_1A_1)_{t+1} = (1 - a_t)f(A_1A_1)_t + a_t(p'_t)^2 \quad \text{and} \quad (20a)$$

$$f(A_1A_2)_{t+1} = (1 - a_t)f(A_1A_2)_t + a_t 2p'_t q'_t, \quad (20b)$$

with p'_t given by (19) and $q'_t = 1 - p'_t$.

Although departures from Hardy-Weinberg are potentially significant for intermediate allele frequencies, the departures are very small when one of the alleles is extremely rare as long as fitnesses do not fluctuate too severely (e.g., alternating generations of lethality for the alternative homozygotes). Under realistic levels of fitness variation, we can ignore the departures from Hardy-Weinberg when deriving the protected polymorphism conditions, as demonstrated by our numerical analyses below. When either allele is rare, the genotype frequencies approximate Hardy-Weinberg and the protection conditions reduce to the haploid case (3) with the rare allele being present only in heterozygotes. The resulting protected polymorphism conditions are

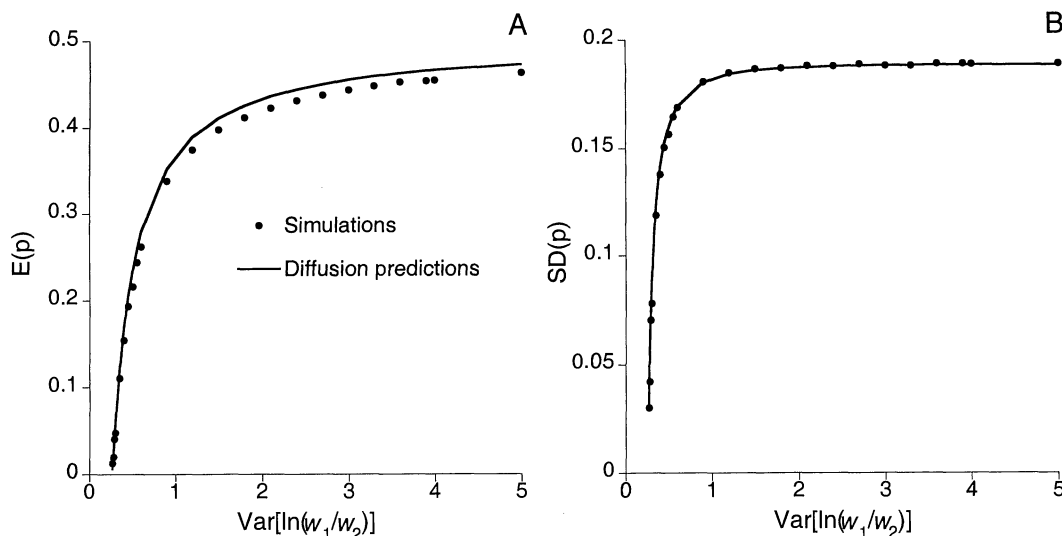


FIG. 4. Comparison of Monte Carlo results (dots) with the diffusion predictions (solid curve) for the mean (A) and SD (B) of allele frequencies under haploid selection. The calculations assume that $a_t \equiv 0.25$ and $\gamma = E[\ln(w_{1,t}/w_{2,t})] = -0.1$, whereas $\sigma^2 = \text{Var}[\ln(w_{1,t}/w_{2,t})]$ ranges from 0.27 to 5. The maximum standard errors for the estimates of the means (SDs) is 0.0037 (0.0049).

$$E \ln \left[1 + a_t \left(\frac{w_{12,t}}{w_{22,t}} - 1 \right) \right] > 0 \quad \text{and} \quad (21a)$$

$$E \ln \left[1 + a_t \left(\frac{w_{12,t}}{w_{11,t}} - 1 \right) \right] > 0. \quad (21b)$$

In preparation for analyzing the *Linanthus* polymorphism, it is useful to consider the special case in which the heterozygote always has intermediate fitness. For simplicity, we will assume that

$$w_{12,t} = hw_{11,t} + (1 - h)w_{22,t} \quad (22)$$

for some fixed dominance parameter h , with $0 < h < 1$. With this simplification, the protected polymorphism conditions (21) become

$$E \ln \left[1 + a_t h \left(\frac{w_{11,t}}{w_{22,t}} - 1 \right) \right] > 0 \quad \text{and} \quad (23a)$$

$$E \ln \left[1 + a_t (1 - h) \left(\frac{w_{22,t}}{w_{11,t}} - 1 \right) \right] > 0. \quad (23b)$$

These are equivalent to the haploid conditions, (4) and (8), with a_t replaced by $a_t h$ when considering protection of allele A_1 and a_t replaced by $a_t(1 - h)$ when considering protection of allele A_2 . As shown in Figure 1, lowering $E(a_t)$ broadens the range of parameter values for which polymorphism is maintained. Given that the dominance parameter effectively lowers $E(a_t)$, conditions (23) show that diploidy with heterozygote intermediacy provides polymorphism-facilitating buffering (as exemplified by Gillespie's [1991, ch. 4.4] SAS-CFF model) that supplements the storage effect provided by the seed bank (cf. Chesson 1985). As $h \rightarrow 1$, corresponding to A_1 becoming increasingly dominant, the sufficient condition for maintaining the nearly recessive allele A_2 in the population (i.e., inequality 23b) converges to the necessary condition

$$E \left[a_t \left(\frac{w_{22,t}}{w_{11,t}} - 1 \right) \right] > 0. \quad (24)$$

The accuracy of these protected polymorphism conditions is discussed below.

Selection on Diploids: Dominance

Assume that allele A_1 is dominant to A_2 , so that $w_{11,t} = w_{12,t} = w_{1,t}$ and $w_{22,t} = w_{2,t}$. The case with a constant has been analyzed numerically by Hedrick (1995), who assumed that genotype frequencies follow Hardy-Weinberg. From condition (23a), we see that the protected polymorphism condition for the dominant allele A_1 is

$$E \ln \left[1 + a_t \left(\frac{w_{1,t}}{w_{2,t}} - 1 \right) \right] > 0, \quad (25)$$

which is identical to the haploid condition (4).

Deriving the protection condition for the recessive allele is more subtle because a linear analysis does not suffice. The arguments of Haldane and Jayakar (1963) and Karlin and Liberman (1975) can be adapted to show that, whenever the departures from Hardy-Weinberg are negligible for $p \approx 1$, the recessive allele is protected whenever

$$E \left[a_t \left(\frac{w_{2,t}}{w_{1,t}} - 1 \right) \right] > 0, \quad (26)$$

which is the necessary condition derived above for the haploid case. This shows that complete recessivity facilitates the maintenance of an allele under this model. Condition (26) also follows as a limit from (23), where the heterozygote has intermediate fitness. Setting $a_t = az_t$, as before, condition (26) can be rewritten as

$$E \left(z_t \frac{w_{2,t}}{w_{1,t}} \right) = E \left(\frac{w_{2,t}}{w_{1,t}} \right) + \text{Cov} \left(z_t, \frac{w_{2,t}}{w_{1,t}} \right) > 1. \quad (27)$$

As in the haploid case, this shows that a positive covariance between favorable conditions (high z_t) and the relative fitness of A_2 can compensate for a low arithmetic mean fitness. If $a_t \equiv 1$, corresponding to no seed bank, the protected polymorphism conditions (25) and (27) reduce to the conditions derived by Haldane and Jayakar (1963).

Diffusion approximation and numerical results

As in the haploid case, we can again obtain a diffusion approximation, but now an additional approximation enters because of the departures from Hardy-Weinberg. We will apply a one-dimensional diffusion approximation, assuming that the genotype frequencies closely approximate Hardy-Weinberg, then present simulation results showing that the resulting predictions for the mean and SD of allele frequencies are quite accurate over a wide range of parameter values.

Proceeding as in the haploid case, the appropriate infinitesimal mean and variance are

$$m(p) = -ap(1 - p)^2 \left[\gamma + \frac{1}{2}\sigma^2 + C - \sigma^2(1 - p)^2 \right] \quad (28a)$$

and

$$v(p) = a^2[p(1 - p)^2]^2\sigma^2, \quad (28b)$$

where

$$\gamma = E \left[\ln \left(\frac{w_{2,t}}{w_{1,t}} \right) \right], \quad (29a)$$

$$\sigma^2 = \text{Var} \left[\ln \left(\frac{w_{2,t}}{w_{1,t}} \right) \right], \quad \text{and} \quad (29b)$$

$$C = \text{Cov} \left[z_t, \ln \left(\frac{w_{2,t}}{w_{1,t}} \right) \right] \quad (29c)$$

(note the change in sign between the definitions of γ in equations 29a-c and 14). The behavior of this diffusion process is determined by a composite parameter, k , defined by

$$k = \frac{\gamma + \frac{1}{2}\sigma^2 + C}{\sigma^2}. \quad (30)$$

A stationary distribution, corresponding to protected polymorphism, exists if and only if

$$0 < k < 1 - \frac{a}{2}, \quad (31)$$

where the first inequality corresponds to protection of the

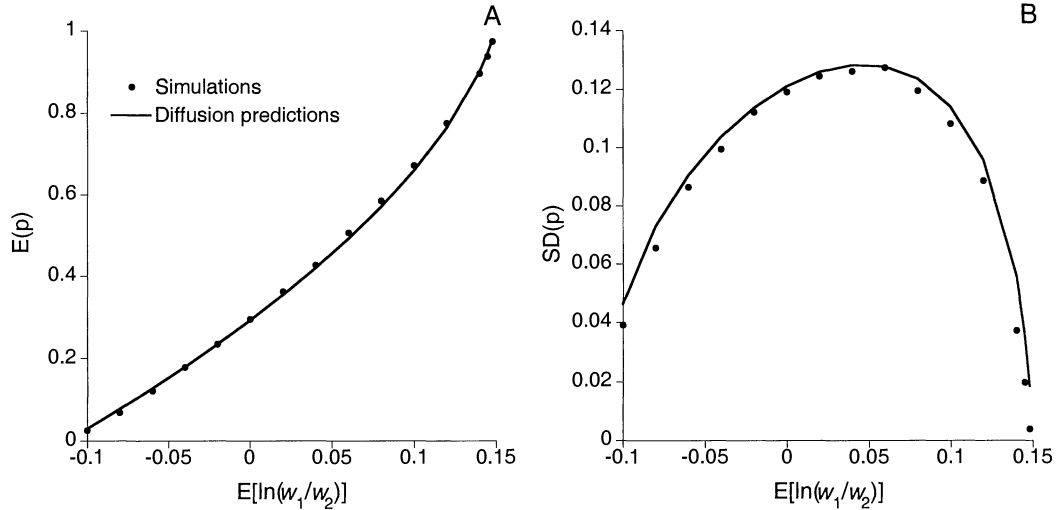


FIG. 5. Comparison of Monte Carlo results (dots) with the diffusion predictions (solid curve) for the mean (A) and SD (B) of allele frequencies under diploid selection with complete dominance. The calculations assume that $a_i \equiv 0.25$ and $\sigma^2 = \text{Var}[\ln(w_{1,i}/w_{2,i})] = 0.3$, whereas $\gamma = E[\ln(w_{1,i}/w_{2,i})]$ ranges from -0.10 to 0.148 . Standard errors for the estimates were obtained from 100 replicates, but were too small to display in the figures—the maximum value was 0.0032 for the means and 0.0018 for the SDs.

recessive allele and the second corresponds to protection of the dominant. The condition for protection of the dominant allele, $k < 1 - (a/2)$, can be rewritten as $\gamma + C < (\sigma^2/2)(1 - a)$, which is identical to condition (15) derived for the haploid model. When $a_i \equiv 1$, the condition for protection of the dominant reduces to Haldane and Jayakar's (1963) condition, $\exp\{E[\ln(w_{2,i}/w_{1,i})]\} < 1$. In other cases, conditions (31) approximate the exact conditions (25) and (27).

When conditions (31) are satisfied, the stationary distribution for the frequency of A_1 is described by Frank's distribution,

$$\phi(p) = \frac{\text{Exp}\left(\frac{2k}{a}\right)\text{Exp}\left(\frac{-2k}{a(1-p)}\right)p^{2[(1-k)/a-1]}(1-p)^{(2k/a)-1}}{\Gamma\left(\frac{2(1-k)}{a}-1\right)U\left(\frac{2(1-k)}{a}-1, 4-\frac{2k}{a}, \frac{2k}{a}\right)}, \tag{32}$$

where $U(x, y, z)$ denotes the second Kummer confluent hypergeometric function (Abramowitz and Stegun 1964, eq. 13.2.6) and $\Gamma(x)$ denotes the gamma function. Its mean and variance are

$$E(p) = 1 - E(1-p) = 1 - \frac{U\left(\frac{2(1-k)}{a}-1, 3-\frac{2k}{a}, \frac{2k}{a}\right)}{U\left(\frac{2(1-k)}{a}-1, 4-\frac{2k}{a}, \frac{2k}{a}\right)} \tag{33}$$

$$\text{Var}(p) = \frac{U\left(\frac{2(1-k)}{a}-1, 2-\frac{2k}{a}, \frac{2k}{a}\right)}{U\left(\frac{2(1-k)}{a}-1, 4-\frac{2k}{a}, \frac{2k}{a}\right)} - [E(1-p)]^2. \tag{34}$$

When $a_i \equiv 1$, corresponding to no seed bank, the model

reduces to the Haldane and Jayakar (1963) model analyzed by Levikson and Karlin (1975) and the moments simplify to

$$E(p) = \frac{1-2k}{1-k} \tag{35a}$$

$$\text{Var}(p) = \frac{k^2(1-2k)}{(1-k)^2}. \tag{35b}$$

Before using these results to discuss the *Linanthus* polymorphism, we will compare the analytical predictions to Monte Carlo results produced by simulating the exact two-dimensional recursions (18)–(20) for genotype frequencies. Sample outcomes are shown in Figures 5 and 6. The simulations followed the procedures used in the haploid examples (Figs. 3 and 4). Despite our Hardy-Weinberg assumption, the one-dimensional diffusion approximation still accurately predicts the means and standard deviations.

APPLICATION TO LINANTHUS

Estimation of Parameters

Schemske and Bierzychudek (2001) have estimated plant density, flower-color frequency, and seed set per plant at a site near Pearblossom, California (Pearblossom site 1) very close to sites surveyed in Epling and Dobzhansky (1942) and Epling et al. (1960). Table 1 presents the data for the 7 years between 1988 and 1999 with nonzero seed set. We will use these to estimate the parameters of our model.

First, we estimate relative fitnesses for each year from relative seed production. The results are reported in the fifth column of Table 1. Next, consider $z_t = a_t/E(a_t)$, the relative year-to-year contributions to the seed bank. Let x_t denote the total number of seeds produced at the site in year t , and let \bar{x} denote the average of the x_t . Using the Table 1 data, we estimate x_t as the product of the number of plants found on three 50×1 -m transects that provided most of the plants for

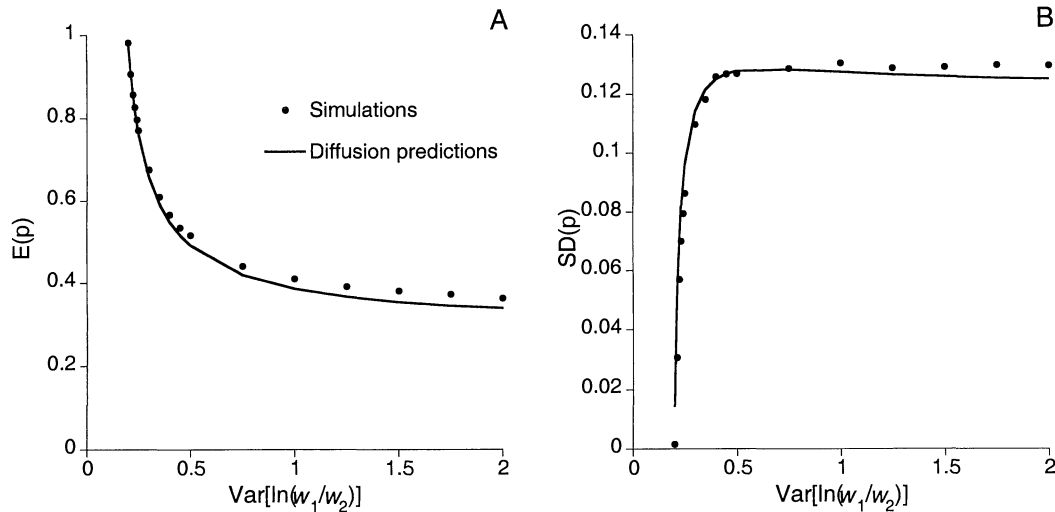


FIG. 6. Comparison of Monte Carlo results (dots) with the diffusion predictions (solid curve) for the mean (A) and SD (B) of allele frequencies under diploid selection with complete dominance. The calculations assume that $a_t \equiv 0.25$ and $\gamma = E[\ln(w_{1,t}/w_{2,t})] = 0.1$, whereas $\sigma^2 = \text{Var}[\ln(w_{1,t}/w_{2,t})]$ ranges from 0.202 to 2. The maximum standard errors for the estimates of the means (SDs) is 0.0037 (0.0023).

the seed set analysis and the average number of seeds per plant (weighted by the phenotype frequencies determined on the transects). We estimate z_t in Table 1 as

$$z_t = \frac{x_t}{\bar{x}} \tag{36}$$

According to our model, the average time that seeds remain dormant is proportional to $1/a$. Epling et al. (1960) reported that plants reappeared on a plot on which no adults had been seen in 10 years. They also performed removal experiments demonstrating that many seeds remain viable for at least 7 years. By comparing seedling densities on their elimination plots to the maximum densities on control plots, Wright (1978, p. 196) argued that seed density declined by more than 50% in 6 years. This implies that $1 - a$ is less than 0.89, so that a is larger than 0.11. However, this estimate of a is demonstrably unreliable and systematically biased upward. For instance, Wright's method (1978, table 6.1) implies that the seed bank was depleted by over 50% within 1 year, but by less than 10% after 4 years. Moreover, his analysis tends to overestimate seed bank depletion by comparing the density of plants on the elimination plots, which were chosen because of high initial densities, to the average density on the *densest square foot* of 260 100-ft² plots. From these data, we conjecture that a is on the order of 0.05 to 0.2, with the lower part of the range being more likely.

Protected Polymorphism?

Assuming that blue's phenotypic dominance implies complete dominance for fitness, results (26) and (27) imply that the conditions for protected polymorphism are

$$E\left(z_t \frac{w_{\text{white},t}}{w_{\text{blue},t}}\right) = E\left(\frac{w_{\text{white},t}}{w_{\text{blue},t}}\right) + \text{Cov}\left(z_t, \frac{w_{\text{white},t}}{w_{\text{blue},t}}\right) > 1 \quad \text{and} \tag{37}$$

$$E \ln \left[1 + a_t \left(\frac{w_{\text{blue},t}}{w_{\text{white},t}} - 1 \right) \right] > 0, \tag{38}$$

where the first condition insures persistence of white and the second insures persistence of blue. Table 1 shows that although $E(w_{\text{white}}/w_{\text{blue}}) < 1$, the critical weighted average, $E(z_t w_{\text{white},t}/w_{\text{blue},t})$, exceeds one, reflecting the fact that whites produce more seeds than blues in high rainfall years that contribute disproportionately to the seed bank. As shown by (5)–(7) above, condition (38) for the persistence of blue can be satisfied only if

$$E\left(z_t \frac{w_{\text{blue},t}}{w_{\text{white},t}}\right) = E\left(\frac{w_{\text{blue},t}}{w_{\text{white},t}}\right) + \text{Cov}\left(z_t, \frac{w_{\text{blue},t}}{w_{\text{white},t}}\right) > 1. \tag{39}$$

As shown in Table 1, the point estimate of this quantity is only 0.92, suggesting that blue may not be stably maintained in this population. There are, however, two sources of statistical uncertainty that must be considered: the precision of the parameter estimates in Table 1 and the extent to which the observed variation in seed set is representative of the long-term variation relevant to this polymorphism.

Table 2 addresses the first source of uncertainty with bootstrap confidence intervals for $E(z_t w_{\text{white},t}/w_{\text{blue},t}) - 1$, $E(z_t w_{\text{blue},t}/w_{\text{white},t}) - 1$, and $E \ln \{ 1 + a z_t [(w_{\text{blue},t}/w_{\text{white},t}) - 1] \}$, using various values of a . The confidence intervals are based on the bias-corrected and accelerated (BC_a) bootstrap method described in Efron and Tibshirani (1993, ch. 14). The bootstraps were performed by resampling the multivariate data on seed production, morph frequencies, and plant densities over years. The resulting confidence intervals for both the necessary, (39), and sufficient, (38), conditions for invasion of blue include values that insure persistence. To check whether *both* alleles can increase when rare, we constructed bootstrap intervals for the product of the two invasion conditions. In more than 25,000 bootstraps with $a = 0$ and $a = 0.2$, no examples were found in which *neither* allele could increase when rare, thus the product of the invasion conditions is positive only when both are positive. Again, the confidence intervals include positive values, indicating that *both* invasion conditions can be simultaneously satisfied.

TABLE 1. *Linanthus* data from Pearblossom, California (Pearblossom site 1 of Schemske and Bierzychudek 2001).

| Year | No. of seeds/plant | | | $\frac{w_{blue}}{w_{white}}$ | % blue ² | % blue seed ³ | Plant density ⁴ | z_t^5 |
|--------------------------|--------------------|--------|----------------------|------------------------------|---------------------|--------------------------|----------------------------|---------|
| | Blue | White | Average ¹ | | | | | |
| 1988 | 30.45 | 19.67 | 21.12 | 1.55 | 13.5 | 19.1 | 2754 | 0.269 |
| 1989 | 5.00 | 3.83 | 3.99 | 1.31 | 13.7 | 17.0 | 233 | 0.004 |
| 1991 | 260.13 | 302.42 | 295.71 | 0.86 | 15.9 | 14.0 | 870 | 1.190 |
| 1992 | 18.58 | 13.28 | 14.06 | 1.40 | 14.7 | 19.1 | 3268 | 0.212 |
| 1993 | 2.77 | 1.12 | 1.29 | 2.47 | 10.4 | 21.6 | 1926 | 0.012 |
| 1995 | 65.62 | 73.35 | 72.46 | 0.89 | 11.6 | 10.5 | 9971 | 3.341 |
| 1998 | 108.87 | 125.81 | 124.29 | 0.87 | 9.0 | 7.9 | 3432 | 1.972 |
| Average | 70.20 | 77.07 | 76.13 | 1.34 | 12.7 | 15.6 | 3208 | 1.000 |
| Average RSN ⁶ | 1.34 | 0.85 | | | | | | |
| Geometric mean RSN | 1.25 | 0.80 | | | | | | |
| Weighted average RSN | 0.92 | 1.10 | | | | | | |

¹ This weights the seed numbers by the frequencies reported in the “% blue” column.
² Frequency estimates for phenotypes are based on complete censuses of blue and white plants in three 50 × 1-m transects associated with the site where seed production was measured (for details, see Schemske and Bierzychudek 2001).
³ This is an approximation for the fraction of seeds carrying a blue allele based on assuming that the parental genotypes follow Hardy-Weinberg frequencies.
⁴ These densities are based on the censuses used to estimate flower-color frequencies.
⁵ The relative contributions to the seed bank in each year were estimated by comparing the average number of seeds produced in each year (the product of the average number of seeds per plant and plant density) to the average number across years.
⁶ Relative seed number, normalized by the number produced by the other morph.

Therefore, the Table 1 data are consistent with the hypothesis that fluctuating selection as modeled above maintains the flower color polymorphism. The robustness of this conclusion will be considered next.

One way to quantify how far the data are from meeting the protected polymorphism conditions is to ask what scaling factor would have to be applied to the relative fitnesses of blue so that (38) would be satisfied. This can be determined by numerically solving

$$E \ln \left[1 + a_t \left(y \frac{w_{blue,t}}{w_{white,t}} - 1 \right) \right] = 0, \quad (40)$$

for y . For $0.05 < a < 0.2$, the result is $y = 1.11$, that is, an 11% increase in the relative fitness of the blues would allow them to increase when rare. If the relative fitnesses of the blues were increased by this amount, white’s relative fitnesses

would be reduced to about 90% of the observed values. With this change, (37) is still satisfied and a protected polymorphism would result.

A second source of uncertainty in our analysis is whether the data in Table 1 are representative of the fluctuations experienced by this population. Over the 11 years of the study, only 7 years had sufficient rain for germination. As noted in Schemske and Bierzychudek (2001), the combined rainfall in March and April gives the highest correlation with mean seed number. Using March plus April rainfall data from the nearby Pearblossom weather station, we can test whether the seven seed-producing years in Table 1 are typical by comparing them to the 10 years from 1944 to 1957 in which Epling et al. (1960, fig. 2) observed flowering plants. The median March plus April rainfall was lower during the flowering years reported in Epling et al. (1960; 4.19 cm vs. 6.04 cm), but not significantly so ($P > 0.5$ from a Wilcoxon rank sum test).

Incomplete dominance.—How sensitive is our coexistence analysis to the assumption that the blue allele has a fully dominant effect on fitness as well as flower color? For simplicity we address this by assuming that heterozygote fitness can be expressed as

$$w_{12,t} = hw_{11,t} + (1 - h)w_{white,t} \quad (41)$$

for some constant h , where w_{11} denotes the fitness of blue homozygotes. Assuming that the adult genotype frequencies do not depart too greatly from Hardy-Weinberg proportions, the fitness of blue individuals can be approximated by

$$w_{blue,t} = p_t w_{11,t} + (1 - p_t) w_{12,t} \quad (42)$$

where p_t is the frequency of the blue allele among flowering plants. For a fixed value of h , we can estimate $w_{11,t}$ for each year by combining (41) and (42), then apply (23) to determine whether the protected polymorphism conditions are satisfied. For $0.5 < h < 1$, the point estimates indicate that blue still cannot invade, but white can. Equation (40) provides a way to quantify the effect of incomplete dominance. We can de-

TABLE 2. Evaluation of the protected polymorphism conditions using the data from Table 1.

| | Point estimate | 95% confidence interval ¹ |
|--|----------------|--------------------------------------|
| White: | | |
| (a) $E(z_t w_{white,t} / w_{blue,t}) - 1$ | 0.104 | (-0.091, 0.143) |
| Blue: | | |
| (b) $E(z_t w_{blue,t} / w_{white,t}) - 1$ (necessary) | -0.076 | (-0.122, 0.194) |
| (c) $E \ln \{ 1 + a_t [(w_{blue,t} / w_{white,t}) - 1] \}$ | | |
| $a = 0.05$ | -0.004 | (-0.006, 0.020) |
| $a = 0.1$ | -0.008 | (-0.012, 0.041) |
| $a = 0.2$ | -0.016 | (-0.025, 0.082) |
| White and blue: (a × b) (necessary) | -0.008 | (-0.183, 0.057) |
| sufficient (a × c) | | |
| $a = 0.05$ | -0.0004 | (-0.0009, 0.00004) |
| $a = 0.1$ | -0.0008 | (-0.0018, 0.00007) |
| $a = 0.2$ | -0.0017 | (-0.0037, 0.00012) |

¹ BC_a bootstrap confidence intervals based on 10,000 bootstrap samples (see Efron and Tibshirani 1993, ch. 14).

TABLE 3. Approximate quantiles of the long-term frequency variation of blue-flowered plants based on the stationary distribution of allele frequencies, (34), for various values of the average frequency of the blue allele, $E(p)$, and average annual contribution to the seed bank, $a = E(a_i)$. For each combination of parameters, the upper interval gives the lower and upper quartiles and the lower interval gives the lower and upper 2.5% quantiles.

| $E(p)$ (% blue flowers) | $a = 0.05$ | $a = 0.1$ | $a = 0.2$ |
|-------------------------------|----------------------------------|----------------------------------|------------------------------------|
| 0.030 (0.059) | (0.031, 0.079) (0.009, 0.150) | (0.019, 0.082) (0.002, 0.197) | (0.005, 0.080) (0.00004, 0.275) |
| 0.065 (0.126) | (0.087, 0.157) (0.042, 0.242) | (0.068, 0.167) (0.020, 0.300) | (0.040, 0.177) (0.003, 0.392) |
| 0.100 (0.190) | (0.145, 0.228) (0.084, 0.320) | (0.123, 0.242) (0.050, 0.381) | (0.087, 0.260) (0.016, 0.477) |

termine the factor by which the fitness of blue heterozygotes must be increased relative to whites for blue to invade. As noted above, with $h = 1$ (blue completely dominant), an 11% relative fitness increase is required. For $h = 0.9$, this is reduced to 10%; and for $h = 0.8$, it is reduced to 9%. Thus, our qualitative and quantitative results concerning protected polymorphism do not depend critically on the assumption of complete dominance.

Fluctuations in phenotype frequencies.—How much frequency variation is expected under our model? Note that the stationary distribution (32) depends on only two parameters, $a = E(a_i)$ and the composite parameter k defined by (30). Thus, once a and the mean allele frequency, $E(p)$, are specified, the stationary distribution of allele frequencies is completely determined. Table 3 gives approximate lower and upper quartiles (25% and 75% quantiles) and 2.5% and 97.5% quantiles of the frequency of blue flowers (ignoring departures from Hardy-Weinberg frequencies) using the stationary distribution (32) determined as a function of $E(p)$ and a for values in the range suggested by the *Linanthus* data. The upper and lower quartiles are comparable to the range of flower-color frequency variation observed in Table 1 only with $a = 0.05$ (and $E[p] = 0.065$). However, part of the discordance is attributable to the fact that the seed bank produces a high autocorrelation in allele frequencies across years, so that only a small fraction of the range predicted in Table 3 would be observed over a decade. Rather than conjecturing a joint distribution for the relevant stochastic processes, we have simulated the short-term dynamics of allele frequencies by bootstrapping the seven estimates of $(z_i,$

$w_{\text{blue},i}/w_{\text{white},i})$ presented in Table 1, using various values of a and initial genotype frequencies. The simulations use the full diploid recursions (18–20), but assume that the seed bank begins with Hardy-Weinberg genotype frequencies. The results are summarized in Table 4 in terms of quantiles of the final frequency of the blue phenotype after seven or 50 seed-producing generations.

Table 4 illustrates several points. First, as expected from the fact that the condition for the protection of the blue allele is not satisfied by our point estimate, the frequency of blue tends to decrease. However, even with a as high as 0.2, the buffering effect of the seed bank insures that phenotype frequencies change very slowly. Indeed, even after 50 seed-producing generations, the polymorphism would be maintained. One way to quantify the rate of decline of blue is to calculate an effective relative fitness, denoted $w_{e(\text{blue})}$, that relates the observed decline in the median allele frequency to the dynamics of a fully deterministic model. Separate estimates of $w_{e(\text{blue})}$ can be obtained for each entry in Table 4, but *all* of them equal 0.92 to two significant digits. Finally, it is notable that the data in Table 1 show a wider range of fluctuations of phenotype frequencies than shown in Table 4, even with $a = 0.2$. This suggests sources of variation not captured by our model.

Adequacy of the Model

Population geneticists rarely have sufficient data to estimate all parameters of a proposed model. Using the estimates in Table 1, we can ask whether the model accurately predicts the changes in morph frequencies reported in Table 1. Despite yearly sample sizes that average 3208, and range from 233 to 9971, only two of the frequency estimates between successive samples are significantly different—the change from 14.7% blue in 1992 to 10.4% in 1993 ($\chi^2_1 = 19.5, P = 10^{-5}$) and the change from 11.6% in 1995 to 9% in 1998 ($\chi^2_1 = 17.6, P < 10^{-4}$). (These changes remain highly statistically significant even after correcting for multiple comparisons.) Both years are preceded by statistically significant levels of selection (Schemske and Bierzychudek 2001), with blues having higher fitness in 1992 and whites having higher fitness in 1995. As expected from (1), the frequency of blue falls in 1998 (the first year after 1995 in which flowers were produced). However, contrary to the prediction of our model, the frequency of blue significantly declines from 1992 to 1993 despite blue’s seed production advantage in 1992. As

TABLE 4. Projected effects of selection based on resampling the empirical estimates of $(w_{\text{blue}}/w_{\text{white}}, z)$ from Table 1. The values given are the median and lower and upper 2.5% quantiles based on 3000 simulations for the final frequency of blue-flowered plants after the indicated number of seed-producing years, starting from various initial frequencies.

| Initial frequency | $a = 0.05$ | $a = 0.1$ | $a = 0.2$ |
|----------------------|----------------------|----------------------|----------------------|
| | 7 years | | |
| 0.126 | 0.123 (0.118, 0.127) | 0.120 (0.110, 0.129) | 0.114 (0.097, 0.132) |
| 0.190 | 0.186 (0.179, 0.192) | 0.182 (0.169, 0.194) | 0.173 (0.147, 0.197) |
| 50 years | | | |
| 0.126 | 0.106 (0.095, 0.117) | 0.089 (0.072, 0.109) | 0.061 (0.038, 0.093) |
| 0.190 | 0.162 (0.146, 0.177) | 0.137 (0.111, 0.165) | 0.095 (0.062, 0.140) |

indicated by our statistical test of homogeneity, the 1992–1993 change in phenotype frequency is not a sampling effect. If we view the 3268 individuals censused in 1992 and the 1926 individuals censused in 1993 as independent binomial samples, the approximate 95% confidence interval for the difference in blue frequencies is (−0.061, −0.024). What can account for this qualitative departure from our predictions?

Our model allows seed viability, germination rates, and seedling viabilities to vary across years but assumes that performance in the seed bank is independent of seed age and genotype and that seedling viability is independent of genotype. In reality, seed viabilities and germination rates surely depend on seed age and may depend on: (1) genotype; (2) interactions of genotype with fluctuating conditions; (3) interactions of genotype with age; and (4) three-way interactions involving genotype, age, and conditions. Similarly, seedling viability may vary with genotype and interactions between genotype and environmental conditions. We have no new data to test any of these possibilities, but reanalysis of the data reported in Epling et al. (1960) suggest significant age effects and/or fluctuating selection prior to seed set.

Unexplained variation in preseed-set performance.—In their figure 10B, Epling et al. (1960) report flower-color frequencies from 1948 to 1954 observed on three polymorphic 100-ft² elimination plots, separated by 50 ft, from which all flowering plants were removed before seed set each year. There are two noteworthy observations in addition to the demonstration of seed bank longevity. First, there are no statistically significant differences between the phenotype frequencies observed in 1948 and 1954 on any of the three plots. In two plots the observed frequency of blue went up insignificantly, but in the third it went down. Thus, as emphasized by Wright (1978, p. 197), there is no evidence for consistent directional selection on seed viability. Second, contrary to Wright's assertion that there were *no* significant changes in the color frequencies over the 5 years, two of the three plots—the ones with the largest sample sizes—show statistically heterogeneous phenotype frequencies (the three samples yield, $\chi^2_3 = 5.2$, $P > 0.2$; $\chi^2_4 = 23.1$, $P < 0.001$; and $\chi^2_4 = 14.5$, $P < 0.01$, respectively). The two sites with variable frequencies are separated by only 50 ft; and for both, the significant heterogeneity is caused by 9% frequency changes between 1952 and 1953. Surprisingly, the frequency of blue significantly increased at one site, but decreased at the other. This suggests fine-scale *spatial* variation in the composition of the seed bank and/or the age- and/or genotype-dependent germination propensities of the seeds. To explain these data solely in terms of genotype-dependent germination differences, the relative germination rate for blue would have to be 1.45 (0.69) to explain the 9% increase (decrease). Similarly, the 1992–1993 frequency data in Table 1 can be explained by a relative germination rate for blue of 0.67. This hypothetical selection is quite intense, but comparable to the fecundity selection documented in Table 1. Interestingly, this scenario requires that in 1993 when the blues had a significant seed set advantage, they had a significant germination rate (or viability) *disadvantage* of comparable magnitude. Alternatively, the unexplained variation may reflect age-dependent germination rates and fluctuations in the genotype frequencies of newly produced seeds, as shown by the column labeled “% blue seed” in Table 1.

Age effects.—Epling et al. (1960) found that germination success declines with seed age, except that 2-year-old seeds germinated more readily than 1-year-old seeds. Variation of germination rates with age is widely documented (e.g., Philippi 1993), and germination delays are expected because new seeds have a germination inhibitor in their seed coats that is only gradually washed out. Variation in germinability is known to depend on many factors, including nongenetic maternal effects (Baskin and Baskin 1998, ch. 8; Fenner 1985, ch. 6). Thus, each cohort could have a different age-specific germination schedule, depending on the pattern of yearly rainfall. If germination rates are strongly age-dependent, with germination rates peaking after several years, the color composition of Epling et al.'s (1960) elimination plots in successive years might reflect morph-specific differences in seed production from distinct cohorts. Even without considering environmental and genetic effects, this generalization—toward the full age-structured model considered by Templeton and Levin (1979)—would require estimates of age-specific germination rates that are not available for *Linanthus*.

Migration.—Another possibility is that the frequency differences reflect rare long-distance dispersal events (mediated perhaps by whirlwinds that are common in the summer or flash floods) from regions with different genetic compositions. This might be plausible if there were populations nearby with quite different phenotype frequencies. However, the mixed composition at this site is typical of the region. The nearest population with a high frequency of blues is 1.5 km away (however, in the same direction, there is a population that is monomorphic for white only 0.5 km away). Although some gene flow may occur at such distances, it could not significantly alter allele frequencies unless local effective population sizes remained extremely small. This hypothesis is inconsistent with the observed long-term stability of phenotype frequencies found by Epling et al. (1960) and Schemske and Bierzychudek (2001) and estimates of Nm from allozyme frequencies (D. W. Schemske and P. Bierzychudek, unpubl. data). Wright (1978, p. 222) also concluded that migration could not explain the observed frequency changes.

DISCUSSION

We have attempted to understand the white versus blue flower-color dimorphism in a population of *L. parryae* in terms of a simple model of natural selection with overlapping generations that captures the fluctuating absolute and relative fitnesses documented in Schemske and Bierzychudek (2001). We presented a series of theoretical analyses leading up to a diploid model with dominance. Our theoretical treatment follows a long tradition of analyzing fluctuating selection and its potential to maintain genetic variation (reviewed by Felsenstein 1976; Hedrick 1986; Gillespie 1991). We have provided analytical conditions for protected polymorphism and used diffusion approximations to describe the long-term properties of these polymorphisms. However, the data documenting intense fluctuating selection and a long-lived seed bank raise novel questions about both using weak-selection diffusion approximations (elaborated in the Appendix) and applying long-term predictions derived from the diffusion.

We have shown that the fluctuating fitnesses estimated

from nature are statistically consistent with maintaining the observed polymorphism. This conclusion relies critically on both the existence of a persistent seed bank and significant variation in yearly seed set. Our analysis makes clear why the white-flowered morph is more common than the blue despite the fact that both the arithmetic and geometric means of white's relative fitnesses are less than one. The key observation is that the white morph produces consistently more seeds than the blues in the years with the heaviest rainfall and highest seed set. These years contribute most to the seed bank and thus to subsequent generations. This provides a simple genetic analog of the species-diversity maintaining storage effect proposed by Chesson and Warner (1981; for a polygenic example, see Ellner and Hairston 1994).

Despite the extreme fluctuations in the observed relative fitnesses, the morph frequencies have changed relatively little. This reflects the strong damping effect of the seed bank (cf. Gottlieb 1974). This damping also implies that even a study that spans more than a decade may be insufficient for studying the range of environmental conditions responsible for the polymorphism or for determining whether the polymorphism is transient or stable. As shown by the numerical results in Tables 3 and 4, the long-term fluctuations predicted by the diffusion's stationary distribution would take well over 50 years to observe with plausible levels of seed longevity. Equally sobering is the fact that thorough studies of adult fitness spanning more than a decade would have to be supplemented by even more elaborate and sustained studies of seed bank demography and selection to understand all of the biology relevant to the transient behavior of this "simple" polymorphism. As demonstrated by the insights that have emerged from the decades of study of Darwin's finches (Grant 1986; Grant and Grant 1989; Grant and Grant 1997), progress in merging evolutionary genetics with ecology may often require such long-term studies.

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APPENDIX

Derivation of the Infinitesimal Mean and Variance

To derive the infinitesimal moments for the haploid model described by (1) and (2), we define the selection coefficient s_t by

$$\frac{w_{1,t}}{w_{2,t}} = 1 + s_t; \tag{A1}$$

and we describe the relative fluctuations in the contributions to the seed bank by

$$a_t \equiv az_t \equiv a(1 + y_t), \tag{A2}$$

where $a = E(a_t)$ and $E(y_t) = 0$. Following the standard diffusion-approximation conventions (Karlin and Taylor 1981, ch. 15, especially pp. 184–188), we assume that for some small value ϵ , the moments of the random variables s_t and y_t satisfy

$$E(s_t) = \mu = O(\epsilon), \quad E(s_t^2) = \sigma^2 = O(\epsilon), \tag{A3a}$$

$$E(y_t^2) = CV_a^2 = O(\epsilon), \quad E(s_t y_t) = C = O(\epsilon), \quad \text{and} \tag{A3b}$$

$$E(s_t^i y_t^j) = o(\epsilon) \quad \text{for } i + j \geq 3, \tag{A3c}$$

where $O(\epsilon)$ denotes a quantity that approaches zero at the same rate as ϵ as $\epsilon \rightarrow 0$, and $o(\epsilon)$ denotes a smaller quantity that approaches zero faster than ϵ . (The complete derivation also requires scaling the generation time; see Turelli 1977; Karlin and Taylor 1981, ch. 15.)

Using (1), the allele frequency dynamics follow

$$\Delta p_t = a_t(p'_t - p_t) \equiv a_t \Delta_s p_t, \tag{A4}$$

where $\Delta_s p_t = p'_t - p_t$ describes the effects of selection in generation t . The diffusion assumptions (A3) allow us to approximate the dynamics by expanding Δp_t in a Taylor series around $s_t = 0$ and $y_t = 0$ and retaining only the second- and lower-order terms. Expanding the haploid expression for $\Delta_s p_t$ in powers of s_t , we see that

$$\Delta p_t = a(1 + y_t)[p_t(1 - p_t)s_t(1 - s_t) + O(s^3)]. \tag{A5}$$

This expansion and assumptions (A3) produce the expressions given in (13) for $m(p) = E(\Delta p_t | p_t = p)$ and $v(p) = \text{Var}(\Delta p_t | p_t = p)$.

The corresponding diffusion for diploid selection with dominance is derived in the same way, except that instead of using (2) to describe selection in (A4), we approximate the effect of selection by assuming that seedlings follow Hardy-Weinberg genotype proportions so that

$$\Delta_s p_t = \frac{p_t(1 - p_t)^2(w_{1,t} - w_{2,t})}{p_t(2 - p_t)w_{1,t} + (1 - p_t)^2w_{2,t}}. \tag{A6}$$

The selection coefficient s_t is again defined by (A1), and the analog of (A5) is

$$\Delta p_t = a(1 + y_t)p_t(1 - p_t)^2s_t\{1 - s_t[1 - (1 - p_t)^2] + O(s^2)\}. \tag{A7}$$

Consistency Criterion for Identifying the Constants in the Infinitesimal Moments

As described in the text, the interpretation of the constants that appear in the infinitesimal moments is ambiguous. This is most easily demonstrated by example. Note, for instance, that under the assumptions (A3),

$$E(s_t y_t) = \text{Cov}(s_t, y_t) = \text{Cov}[\ln(1 + s_t), y_t] + o(\epsilon). \tag{A8}$$

Because the infinitesimal moments involve only the leading-order terms, the constant C in the infinitesimal mean (13a) might plausibly be interpreted as either $\text{Cov}(w_{1,t}/w_{2,t}, z_t)$ or $\text{Cov}[\ln(w_{1,t}/w_{2,t}), z_t]$. In the limit as $\epsilon \rightarrow 0$, this choice makes no difference. However, what we want to understand is not the limiting case, but actual data whose dynamics are described by the discrete-time stochastic process with appreciable selection and appreciable fluctuations. For the data in Table 1, $\text{Cov}(w_{1,t}/w_{2,t}, z_t) = -0.50$, whereas $\text{Cov}[\ln(w_{1,t}/w_{2,t}), z_t] = -0.38$, so the interpretation of C can significantly affect our predictions. Similarly, σ^2 might be interpreted as $E\{[(w_{1,t}/w_{2,t}) - 1]^2\}$, $\text{Var}(w_{1,t}/w_{2,t})$, or $\text{Var}[\ln(w_{1,t}/w_{2,t})]$, because all three differ only by terms that are $o(\epsilon)$ according to (A3).

We propose the following consistency criterion for identifying the constant: The diffusion approximation should be the same whether selection is quantified by

$$\frac{w_{1,t}}{w_{2,t}} = 1 + s_t \quad \text{or} \tag{A9a}$$

$$\frac{w_{2,t}}{w_{1,t}} = 1 + \tilde{s}_t. \tag{A9b}$$

We will first show that both parameterizations lead to the same diffusion when assumptions (A3) are met, then show how these calculations lead to a specific choice for the constants. Define μ , σ^2 , and C as in (A3). We can make analogous assumptions concerning \tilde{s}_t and define

$$E(\tilde{s}_t) = \tilde{\mu} = O(\epsilon), \quad E(\tilde{s}_t^2) = \tilde{\sigma}^2 = O(\epsilon), \tag{A10a}$$

$$E(y_t^2) = CV_a^2 = O(\epsilon), \tag{A10b}$$

$$E(\tilde{s}_t y_t) = \tilde{C} = O(\epsilon), \quad \text{and} \tag{A10c}$$

$$E(\tilde{s}_t^i y_t^j) = o(\epsilon) \quad \text{for } i + j \geq 3. \tag{A10c}$$

The expansion analogous to (A5) is

$$\Delta p_t = -a(1 + y_t)p_t(1 - p_t)[\tilde{s}_t(1 - \tilde{s}_t + p_t\tilde{s}_t) + O(\tilde{s}^3)]. \tag{A11}$$

The corresponding infinitesimal moments are

$$\bar{m}(p) = ap(1 - p)\left(\tilde{\gamma} + \tilde{C} + \frac{1}{2}\tilde{\sigma}^2 - \tilde{\sigma}^2 p\right) \quad \text{and} \tag{A12a}$$

$$\bar{v}(p) = a^2\tilde{\sigma}^2[p(1 - p)]^2, \tag{A12b}$$

with $\tilde{\gamma} = \tilde{\mu} - \frac{1}{2}\tilde{\sigma}^2$. To reconcile the alternative expressions for the infinitesimal moments, note that

$$\frac{w_{2,t}}{w_{1,t}} = 1 + \tilde{s}_t = \frac{1}{1 + s_t} = 1 - s_t + s_t^2 + O(s^3). \tag{A13}$$

Thus,

$$\tilde{\mu} = -\mu + \sigma^2, \tag{A14a}$$

$$\tilde{\sigma}^2 = \sigma^2, \tag{A14b}$$

$$\tilde{C} = -C, \quad \text{and} \tag{A14c}$$

$$\tilde{\gamma} = -\gamma. \tag{A14d}$$

Using these, it follows that

$$m(p) = \tilde{m}(p) \quad \text{and} \quad (\text{A15a})$$

$$v(p) = \tilde{v}(p). \quad (\text{A15b})$$

Hence, in the weak-selection, small-fluctuation limit, the alternative parameterizations of selection, (A9), produce identical results.

This does not tell us what to do with our data, however. As noted above, (A3) and (A10) seem compatible with setting

$$\mu = E(w_{1,t}/w_{2,t}) - 1, \quad \sigma^2 = \text{Var}(w_{1,t}/w_{2,t})$$

$$C = \text{Cov}(w_{1,t}/w_{2,t}, z_t), \quad \text{or} \quad (\text{A16a})$$

$$\tilde{\mu} = E(w_{2,t}/w_{1,t}) - 1, \quad \tilde{\sigma}^2 = \text{Var}(w_{2,t}/w_{1,t}),$$

$$\tilde{C} = \text{Cov}(w_{2,t}/w_{1,t}, z_t). \quad (\text{A16b})$$

However, these moments will not generally satisfy (A14), so the resulting infinitesimal means and variances (and consequently the predictions for $E[p]$ and $\text{SD}[p]$) will differ depending on whether (A16a) or (A16b) are used. Our consistency criterion suggests that the coefficients should be *defined* so that

$$\tilde{\gamma} = -\gamma, \quad (\text{A17a})$$

$$\tilde{\sigma}^2 = \sigma^2, \quad \text{and} \quad (\text{A17b})$$

$$\tilde{C} = -C. \quad (\text{A17c})$$

This leads to the choices

$$\gamma = E\left[\ln\left(\frac{w_{1,t}}{w_{2,t}}\right)\right], \quad \sigma^2 = \text{Var}\left[\ln\left(\frac{w_{1,t}}{w_{2,t}}\right)\right],$$

$$C = \text{Cov}\left[z_t, \ln\left(\frac{w_{1,t}}{w_{2,t}}\right)\right] \quad \text{and} \quad (\text{A18a})$$

$$\tilde{\gamma} = E\left[\ln\left(\frac{w_{2,t}}{w_{1,t}}\right)\right], \quad \tilde{\sigma}^2 = \text{Var}\left[\ln\left(\frac{w_{2,t}}{w_{1,t}}\right)\right],$$

$$\tilde{C} = \text{Cov}\left[z_t, \ln\left(\frac{w_{2,t}}{w_{1,t}}\right)\right], \quad (\text{A18b})$$

discussed in the text (see eq. 14).