

## Diffusion Analysis and Stationary Distribution of the Two-Species Lottery Competition Model

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The lottery model is a stochastic population model in which juveniles compete for space. Examples include sedentary organisms such as trees in a forest and members of marine benthic communities. The behavior of this model appears to be characteristic of that found in other sorts of stochastic competition models. In a community with two species, it was previously demonstrated that coexistence of the species is possible if adult death rates are small and environmental variation is large. Environmental variation is incorporated by assuming that the birth rates and death rates are random variables. Complicated conditions for coexistence and competitive exclusion have been derived elsewhere. In this paper, simple and easily interpreted conditions are found by using the technique of diffusion approximation. Formulae are given for the stationary distribution and means and variances of population fluctuations. The shape of the stationary distribution allows the stability of the coexistence to be evaluated. © 1989 Academic Press, Inc.

### INTRODUCTION

Several models have been developed to investigate the question of coexistence of competing species in a variable environment. Turelli (1978, 1981) and Turelli and Gillespie (1980) studied a stochastic version of the Lotka-Volterra equations and found environmental fluctuations to have little effect. In contrast, coexistence of species in the lottery model (Chesson and Warner, 1981; Chesson, 1982) was found to be enhanced by environmental variability, provided environmental variability effected birth rates

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and generations were overlapping. Since then a variety of other stochastic models have predicted coexistence as a result of environmental fluctuations (Abrams, 1984; Chesson, 1983, 1984; Shmida and Ellner, 1984).

Chesson (1986, 1988) showed how these different models and their qualitative predictions can be understood in a common framework. The lottery model is the best known of these models. It has the advantage of approximating some of the key features of communities of sessile organisms, which have featured prominently in ecological debate, as reviewed by Fagerstrom (1988) and discussed below. Moreover, the model is simple and its formulation is easily understood, yet by variation of the parameter values this model is capable of exhibiting the full range of qualitative behavior exhibited by the broad class of models to which it belongs, and many of its properties have proved generalizable (Chesson, 1986, 1988).

The lottery model was formulated specifically for organisms that compete for space and makes the assumption that this competition is concentrated during a relatively short period of time as the organisms mature. Competition among adults is assumed to be unimportant, or, if present at all, is of the special sort discussed below that affects only reproduction, not adult survival. The chief findings of the lottery model are that temporal fluctuations in birth rates (or similar parameters affecting recruitment to the adult population) promote coexistence provided generations are overlapping and death rates do not fluctuate too greatly with time. If adult death rates can be large, fluctuations in adult death rates tend to promote competitive exclusion. This latter conclusion is clearest when results of the general model in Chesson (1986, 1988) are taken into account.

The idea that fluctuations in birth rates may promote coexistence in organisms with overlapping generations was generalized to the hypothesis that coexistence is promoted by fluctuations in recruitment to a robust stage in the life-cycle, i.e., a stage with a low mortality rate relatively insensitive to fluctuations in environment and competition. Particular examples include the adults of many species and seeds in the seed bank of many annual plant species (Chesson, 1984; Shmida and Ellner, 1984). Promotion of coexistence in these circumstances is referred to as the storage effect (Warner and Chesson, 1985). The storage effect has attracted attention as a possible mechanism of coexistence in a variety of systems including coral reef fishes (Chesson and Warner, 1981), rainforests (Leigh, 1982; Warner and Chesson, 1985), *Eucalyptus* forests (Comins and Noble, 1985), and may have broad applications to communities of sessile organisms (Silvertown and Law, 1987; Fagerstrom, 1988).

One difficulty with the theory is that conclusions from models have mostly been qualitative, for example implying that coexistence will occur

with sufficient variability in some parameter without quantifying the sufficient amount. Therefore, it has not been possible to assess the strengths of the predicted effects, which are especially important for assessing their significance in nature.

A second difficulty is that very little information is available on the population fluctuations exhibited by coexisting species in these models. While predictions about population fluctuations are an important goal alone, they also have implications for the strength of coexistence and how long it can be expected to last (Chesson, 1982). Moreover, such predictions are needed if there is to be any resolution of the debate about the extent to which population fluctuations of coexisting organisms can be used to distinguish between equilibrium and nonequilibrium mechanisms of coexistence (Herbold, 1984; Rahel *et al.*, 1984; Yant *et al.*, 1984). When the probability distributions of population size in a stochastic population model converge to a unique distribution, called the stationary distribution, that distribution describes the long-run frequencies with which different population sizes are observed. In particular, it defines the mean and variance of population size over time. However, information on stationary distributions for these models is very limited (Chesson, 1984).

Apart from Lotka–Volterra models in which environmental variability has equivocal effects on coexistence (Turelli and Gillespie, 1980), the best quantitative information is available for the lottery model (Chesson and Warner, 1981; Chesson, 1982, 1984, 1985). Moreover, it is the only stochastic competition model for which there is any understanding of the stationary distribution. However, there remain many gaps in our understanding of these aspects of the lottery model. By using a diffusion approximation, this article provides simple and explicit formulae defining the stationary distribution. In doing so, we are providing needed information about an important model that seems reasonably representative of a broader class of models.

### THE MODEL

In the lottery model, we define  $P_i(t)$  as the total proportion of space occupied by species  $i$  at time  $t$ ,  $\beta_i(t)$  as the per capita reproduction, and  $\delta_i(t)$  as the adult death rate of species  $i$  during the interval  $(t, t + 1]$ . Then the equation for the proportion of adults at time  $t + 1$  in the two-species lottery model is

$$P_i(t + 1) = [1 - \delta_i(t)] P_i(t) + [\delta_1(t) P_1(t) + \delta_2(t) P_2(t)] \times \frac{\beta_i(t) P_i(t)}{\beta_1(t) P_1(t) + \beta_2(t) P_2(t)} \quad (1)$$

for  $i = 1, 2$ . In Eq. (1),  $[1 - \delta_i(t)] P_i(t)$  is the proportion of adults of species  $i$  surviving from time  $t$  to time  $t + 1$ . The proportion of new sites available for settling by juveniles is  $[\delta_1(t) P_1(t) + \delta_2(t) P_2(t)]$ , which is the proportion of space given up by adult death. This space is divided among the juveniles of different species in proportion to their abundance. The lottery aspect of the model comes from the fact that  $\beta_i(t) P_i(t) / [\beta_1(t) P_1(t) + \beta_2(t) P_2(t)]$  is the proportion of available space that is secured by juveniles of species  $i$ .

While  $\beta$  is described as a birth rate above, there is considerable latitude in its interpretation. It could easily include juvenile mortality before the stage at which competition occurs among juveniles, and as pointed out by Chesson and Warner (1981), it could also include the relative abilities of juveniles of different species at competition for space. In the latter case, the lottery is biased. Moreover, in a very similar way  $\beta$  could reflect relative competitive abilities of adults; for example, if there is in effect biased lottery competition for finite resources necessary for reproduction.

In the model an important quantity is

$$\rho(t) = \frac{\beta_1(t)/\delta_1(t)}{\beta_2(t)/\delta_2(t)}, \quad (2)$$

which compares the ratios of birth rates and death rates for the two species. For coexistence,  $\rho$  must fluctuate on either side of 1 by a sufficient amount (Chesson and Warner, 1981; Chesson, 1982), as a consequence of fluctuations in birth rates, and possibly combined with death-rate fluctuations.

By using a diffusion approximation we obtain formulae giving necessary and sufficient conditions for the existence of a stationary distribution for  $P_1(t)$  on the interval  $(0, 1)$ . This stationary distribution for  $P_1(t)$  means that  $P_2(t)$  also has a stationary distribution on the interval  $(0, 1)$  and that the two species coexists in the sense of stochastic boundedness (Chesson, 1982). Although existence of the stationary distribution and stochastic boundedness are not always equivalent, they are for the diffusion models discussed here. Thus, we use existence of the stationary distribution as our definition of coexistence.

A diffusion process is a continuous-time process and is characterized by its infinitesimal mean and variance, defined as

$$\mu(x) = \lim_{\varepsilon \downarrow 0} \frac{1}{\varepsilon} E[P_1(t + \varepsilon) - P_1(t) | P_1(t) = x] \quad (3)$$

and

$$\sigma^2(x) = \lim_{\varepsilon \downarrow 0} \frac{1}{\varepsilon} E[\{P_1(t + \varepsilon) - P_1(t)\}^2 | P_1(t) = x], \quad (4)$$

respectively (Karlin and Taylor, 1981). Diffusion approximation of the lottery model involves converting it to continuous time. To do this, the time scale is accelerated by increasing the number of breeding seasons per unit time while decreasing the amount of change taking place in a season. In the lottery model, this is done by letting  $X(t) = \ln \rho(t)$  and assuming  $E[X(t)] = \varepsilon\mu$  and  $\text{Var}[X(t)] = \varepsilon\sigma^2$ ,  $\varepsilon > 0$ . This slows down both deterministic and stochastic change. In addition, we define  $\delta_i(t) = d_i e^{Y_i(t)}$  and assume  $E[Y_i(t)] = 0$  ( $d_i$  is the geometric mean of  $\delta_i(t)$ ),  $\text{Cov}[Y_1(t), X(t)] = \varepsilon\theta_1$ , and  $\text{Cov}[Y_2(t), -X(t)] = \varepsilon\theta_2$ . Higher order central moments are assumed to be  $o(\varepsilon)$ . These definitions decrease the amount of change taking place from one season to the next as  $\varepsilon$  is reduced. To change the number of seasons per unit time,  $P_i(t + \varepsilon)$  is substituted for  $P_i(t + 1)$  in the left hand side of Eq. (1).

In the Appendix, regularity conditions are imposed on the distribution of  $(X(t), Y_1(t), Y_2(t))$  and (3) and (4) are evaluated for the discrete-time lottery model, where  $\varepsilon$  adjusts the time scale and other effects as described above. It follows from Stroock and Varadhan (1979, Theorem 11.2.3) that the lottery model converges weakly to a diffusion process with infinitesimal mean and variance given by

$$\mu(x) = \frac{d_1 d_2 x(1-x)}{[d_1 x + d_2(1-x)]^2} \{d_1 x[\mu - \theta_2 - \sigma^2/2] + d_2(1-x)[\mu + \theta_1 + \sigma^2/2]\} \tag{5}$$

and

$$\sigma^2(x) = \frac{[d_1 d_2 \sigma x(1-x)]^2}{[d_1 x + d_2(1-x)]^2} \tag{6}$$

An interesting feature of  $\mu(x)$  is that whenever  $\mu + \theta_1 + \sigma^2/2 > 0$  and  $\mu - \theta_2 - \sigma^2/2 < 0$ ,  $\mu(x)$  will be positive for low values of  $x$  and negative for high values of  $x$ . Thus this diffusion process can have a mean drift away from both boundaries toward the center, but this is only possible when  $\sigma^2 > 0$ , i.e., it can only occur when  $\rho(t)$  fluctuates over time. A mean tendency to drift away from the boundaries does not guarantee a stable coexistence, however, because at low density the population growth is multiplicative, not additive. This means that mean tendencies on a log scale provide a more appropriate indication of actual population growth. By calculating the infinitesimal mean,  $v(x)$ , and variance,  $\phi^2(x)$ , of  $\ln P_1(t) - \ln P_2(t)$ , we can gain an accurate indication of population growth over the full range of  $x$  values from 0 to 1. For simplicity, we do this just for the case where the adult death rates,  $\delta_i$ , are nonrandom and equal to the value

*d.* The transformation formulae in Karlin and Taylor (1981) yield the remarkable result

$$v(x) = d\{\mu + \sigma^2(1-d)(1-2x)/2\} \quad (7)$$

and

$$\phi^2(x) = d^2\sigma^2, \quad (8)$$

where  $x$  has not been transformed and still represents a point in the space of  $P_1(t)$ . This result shows that the process has constant infinitesimal variance on this log ratio scale. Because  $x$  refers to the original rather than transformed scale, these are not the infinitesimal mean and variance of an Ornstein-Uhlenbeck process; instead, the infinitesimal mean reveals a central tendency linear in  $x$  and reminiscent of logistic growth. In spite of this phenomenological resemblance to logistic growth, the central tendency, which is created by the term  $\sigma^2(1-d)(1-2x)/2$ , exists as a consequence of environmental variability, because it is zero unless  $\sigma^2 > 0$ . Thus, we see a central tendency created by stochastic, not deterministic forces. Overlapping generations, as measured by  $(1-d)$ , are also necessary for this central tendency.

The central tendency in  $v(x)$  is opposed by the term  $\mu$  representing the mean tendency of the environment to favor species 1 over species 2. The term  $\sigma^2(1-d)(1-2x)/2$  by itself creates a tendency to drift toward the value  $P_1(t) = 1/2$ , but when  $\mu$  is not zero there will be a bias away from this value. As we shall see below in Eq. (11), the comparison between  $\mu$  and the quantity  $\sigma^2(1-d)/2$ , giving the magnitude of the central tendency, determines coexistence in this model.

#### THE STATIONARY DISTRIBUTION

The diffusion process determined by (5) and (6) has state space  $(0, 1)$ . In order to show the existence of a stationary distribution, it is necessary to investigate the boundary behavior of the process. In the Appendix it is shown that the boundaries 0 and 1 are natural boundaries, in Feller's terminology (Karlin and Taylor, 1981), which means that the process can reach neither boundary in finite mean time, nor can it be started from either boundary. The conditions for a process with natural boundaries to have a stationary distribution are given by Mandl (1968, Chap. IV, Theorem 7). These conditions are evaluated for the lottery model in the Appendix. To state the results we introduce the quantities

$$\gamma_1 = \frac{2(\mu + \theta_1)}{\sigma^2} \quad \text{and} \quad \gamma_2 = \frac{2(-\mu + \theta_2)}{\sigma^2}. \quad (9)$$

Then the conditions for a stationary distribution can be stated as

$$d_1 < \gamma_1 + 1 \quad \text{and} \quad d_2 < \gamma_2 + 1. \tag{10}$$

The quantities  $\gamma_1$  and  $\gamma_2$  can be considered as measuring for each species its mean relative competitive ability divided by the environmental variance. To see this note that  $\mu = E[\ln \rho] = E[\ln \beta_1/\delta_1 - \ln \beta_2/\delta_2]$ , and so it reflects mean demographic differences between the species. In the  $\gamma_i$ , these mean tendencies are adjusted by the covariance of  $\ln \rho$  with the adult death rate. Condition (10) thus shows that if the  $d_i$  are less than 1, coexistence necessarily occurs as  $\sigma^2$  is increased, making the  $\gamma_i$  small. In addition, if one of the  $d_i$ 's is 1, e.g., if  $d_1 = 1$ , then coexistence can still occur if  $\mu > 0$ , provided  $|\gamma_2|$  is sufficiently small. The latter situation can occur with large enough  $\sigma^2$ . The conditions for the existence of a stationary distribution, Eq. (10), can be stated in the alternative form

$$\sigma^2 > 2 \max \left[ \frac{-(\mu + \theta_1)}{(1 - d_1)}, \frac{-(-\mu + \theta_2)}{(1 - d_2)} \right], \tag{11}$$

which also shows how increases in  $\sigma^2$  must inevitably lead to coexistence provided that the  $d_i$ 's are less than 1. When the stationary distribution exists, the methods of Karlin and Taylor (1981) yield the formula for the density

$$\psi(x) = c [d_1 x + d_2(1 - x)]^2 x^{v_1 - 1} (1 - x)^{v_2 - 1}, \tag{12}$$

where

$$v_1 = \frac{(\gamma_1 + 1)}{d_1} - 1, \quad v_2 = \frac{(\gamma_2 + 1)}{d_2} - 1, \tag{13}$$

and  $c$  is a constant such that  $\int \psi(x) dx = 1$ . Note that this density is the product of a quadratic and a beta density.

The first and second moments of the stationary distribution are

$$E(X) = \frac{v_1 [d_1^2(v_1 + 2)(v_1 + 1) + 2d_1 d_2(v_1 + 1)(v_2) + d_2^2(v_2 + 1)(v_2)]}{(v_1 + v_2 + 2) [d_1^2(v_1 + 1)(v_1) + 2d_1 d_2(v_1)(v_2) + d_2^2(v_2 + 1)(v_2)]} \tag{14}$$

and

$$E(X^2) = \frac{\left( v_1 [d_1^2(v_1 + 3)(v_1 + 2)(v_1 + 1) + 2d_1 d_2(v_1 + 2)(v_1 + 1)(v_2)] + d_2^2(v_1 + 1)(v_2 + 1)(v_2) \right)}{\left( (v_1 + v_2 + 3)(v_1 + v_2 + 2) [d_1^2(v_1 + 1)(v_1)] + 2d_1 d_2(v_1)(v_2) + d_2^2(v_2 + 1)(v_2) \right)}. \tag{15}$$

The shape of the density is important because it yields information about the type of population fluctuations which the two species will experience. For example, if  $d_1 = d_2 = d$ , then the density is a beta distribution, for which the shape can easily be determined based on the parameters  $v_1$  and  $v_2$  (Devore, 1982). When  $v_1 > 1$  and  $v_2 > 1$ , the distribution is zero at 0 and 1 and rises to a unique mode between 0 and 1. For this case, the proportion of space occupied by either species is unlikely to be very small or large and thus stable coexistence of the two species occurs. When  $v_1 > 1$  and  $v_2 < 1$  or  $v_1 < 1$  and  $v_2 > 1$ , then the distribution either increases from zero to  $\infty$  or decreases from  $\infty$  to zero, respectively, as the proportion of space occupied by one species varies from 0 to 1. This is the case of the infinite mode and is not a very stable type of coexistence because it is likely that the proportion of space occupied by a given species will be either small or large relative to the other species at any given time. The beta distribution can also have a U-shape between 0 and 1 and this occurs if  $v_1 < 1$  and  $v_2 < 1$ . Because of reasons similar to those given above, this results in the most unstable form of coexistence. When  $d_1 \neq d_2$ , the essential character of these findings remains unchanged except that an additional interior mode can be introduced if the death rates are markedly different.

It is important to note that, when the stationary distribution exists, its shape is strongly controlled by the geometric mean adult death rates, the  $d_i$ . If the  $d_i$  are small, the  $v_i$  will necessarily be large and the distribution will be concentrated about the mean, leading to highly stable coexistence. Furthermore, if  $\sigma^2$  is large, the  $\gamma_i$  will be small and  $v_i \approx d_i^{-1} - 1$ . Thus for large  $\sigma^2$ , the only features of the biology of the organisms that matter are the adult death rates. Therefore the adult death rates are the most critical parameters determining the nature of population fluctuations of species coexisting in the lottery model.

#### COMPARISON WITH OTHER MODELS

Our results can be compared with those of Chesson and Warner (1981) for the discrete-time lottery model. Their Fig. 1, whose results are represented in Fig. 1 of this paper, presents conditions for coexistence derived numerically under the assumption of equal, nonrandom adult death rates with  $\rho$  having a lognormal distribution. Corresponding to that situation, our results give the condition for coexistence:  $\sigma^2 > 2|\mu|/(1-d)$ . This condition is represented by dashed lines in Fig. 1. The close correspondence attests to the accuracy of the diffusion approximation.

Chesson and Warner also derived the conditions for coexistence for the case of small adult death rates, but arbitrary distributions for birth rates and death rates. The conditions are  $E[\delta_1(t)\{\rho(t) - 1\}] > 0$  and  $E[\delta_2(t)$



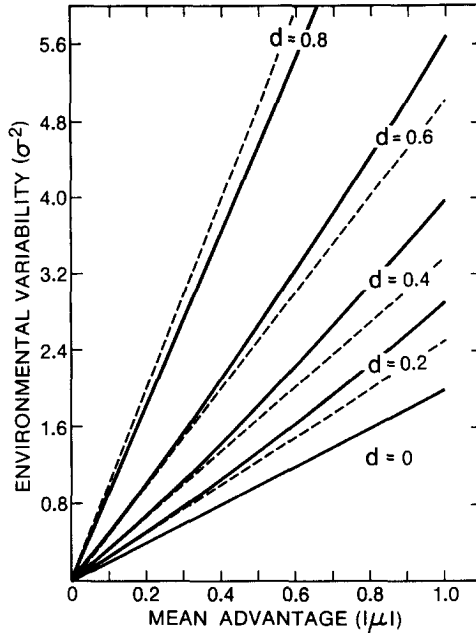


FIG. 1. Comparison of the coexistence conditions of Eq. (11) (dashed lines) with the numerical calculations of Chesson and Warner (1981) (solid lines) for different values of the geometric mean death rate,  $d$ . Note that for  $d=0$  both conditions are identical. The coexistence region for a given  $d$  is the area above the line specified by that particular  $d$ .

$\{\rho^{-1}(t) - 1\}] > 0$ . If  $X(t)$  and  $Y_i(t)$  are normal random variables, then these conditions become  $\sigma^2 > 2 \max[-(\mu + \theta_1), -(-\mu + \theta_2)]$  (see Appendix), which agree precisely with the results of the diffusion approximation for small  $d_i$ 's.

Finally, Chesson (1982) derived shape criteria for the model for large (effectively infinite)  $\sigma^2$ . We noted above that in that case  $v_i \approx d_i^{-1} - 1$ , which then determines the shape of the distribution. The conditions on the shape derived from this are in exact accordance with the conditions derived by Chesson for the discrete-time model. Chesson also derived the shape in situations where both  $\mu$  and  $\sigma^2$  are possibly large, but comparison with that case is complicated. In all cases where comparisons are available, agreement with the diffusion approximation is good.

To obtain a diffusion process from the lottery model (which is a discrete-time Markov process) we speed up the time scale by increasing the number of breeding seasons per unit time, but decrease the amount of change that can take place for each season. There are several ways of decreasing the amount of change that can take place over a season, of which just one method is used here. The primary technique here is to let the quantity  $\rho$

approach 1. This means that the birth-rate/death-rate ratios ( $\beta_i/\delta_i$ ) of the species approach equality so that the competitive advantage that either species has over the other at any time is small. The geometric mean adult death rates are kept constant in time, which means that the mean lifetime of an adult remains constant when measured in units of seasons, but in fact decreases in units of time.

An alternative method used by Chesson (1982, 1984, 1985) does not alter the value of  $\rho$  but decreases the adult death rate to 0, thus making the organisms more long-lived in terms of breeding seasons but not in terms of units of time. However, the biologically important quantity is the number of breeding seasons that an organism lives. Adjustment of the timescale is merely a mathematical device to get a diffusion approximation. Therefore this alternative method is generally regarded as an approximation applicable to long-lived organisms. In this approximation it is also necessary to magnify the population variables  $P_i(t)$  about their mean values because as the death rates approach 0 the stationary distribution converges on its mean. In essence, the variance of the stationary distribution is proportional to the adult death rates, which are approaching 0. The stationary distributions derived from this method are always normal but take account of the actual distributions of the birth rates and death rates, not just the first two moments. In contrast, the approximation in this paper depends only on the first and second order moments of the random variables. As noted above, it tends to agree with results for long-lived organisms when the adult death rates are small. In particular, the beta distribution converges on the normal distribution as the  $d_i$  approach 0, in agreement with Chesson's approximation for long-lived organisms.

The most important feature of the new approximation is that it is not restricted in application to long-lived organisms and does not require altering the scale of  $P_i(t)$  about its mean to obtain a stationary distribution. Thus a distribution on the interval (0, 1) is obtained. Moreover, while the derivation assumes that certain means and variances become small, comparison of the conditions for coexistence derived from the discrete-time model (above) indicates that these assumptions do not restrict the applicability of the results. The approximation is best when the various population parameters involved have lognormal distributions. Comparison of the results on the stationary distribution for large variability also suggests that features of the stationary distribution, in addition to conditions for coexistence, can be trusted far outside the assumptions of their derivations.

When  $d_1 = d_2$ , our diffusion approximation is the same form as that found by Gillespie (1977, 1980) for a model of natural selection of genetic alleles in a random environment. Although the diffusion processes are quite similar, the underlying assumptions that we make are somewhat different

from those made in the genetics literature. In the lottery model important nonlinearities, essential for the form of the diffusion model and for coexistence, are created by overlapping generations. The corresponding models in the genetics literature assume nonoverlapping generations, but important nonlinearities are introduced by a diploid or polyploid genetic structure and possibly nonlinear fitness functions. The lottery model can be put in a genetical context by assuming a haploid genetic system in which the  $P_i$  are the allele frequencies. It then shows that population limitation at the time of recruitment to the adult population coupled with fluctuating selection intensities, resulting from purely temporal fluctuations in fecundity or juvenile survival, can maintain a haploid or asexual polymorphism. This is a new result.

The genetics literature approaches the diffusion approximation a little differently, and to compare our results directly with Gillespie's for the case of constant adult death rates, we would define  $\beta_i(t)/d_i = 1 + X_i(t)$ ,  $E[X_i(t)] = \varepsilon\mu_i$ ,  $\text{Var}[X_i(t)] = \varepsilon\sigma_i^2$ , and  $\text{Cov}[X_1(t), X_2(t)] = \varepsilon\theta_{12}$ . These assumptions lead to a diffusion process with the infinitesimal coefficients

$$\begin{aligned} \mu(x) = & \frac{d_1 d_2 x(1-x)}{[d_1 x + d_2(1-x)]^2} \{d_1 x[\mu_1 - \mu_2 - \sigma_1^2 + \theta_{12}] \\ & + d_2(1-x)[\mu_1 - \mu_2 + \sigma_2^2 - \theta_{12}]\} \end{aligned} \tag{16}$$

and

$$\sigma^2(x) = \frac{[d_1 d_2 x(1-x)]^2 [\sigma_1^2 + \sigma_2^2 - 2\theta_{12}]}{[d_1 x + d_2(1-x)]^2} \tag{17}$$

Although (16) and (17) appear to be different from the infinitesimal coefficients given in (5) and (6), they are in fact identical when one considers that we used the log scale to derive (5). Note that  $\varepsilon\mu = E[\ln \rho(t)] = \varepsilon[\mu_1 - \mu_2 + (\sigma_2^2 - \sigma_1^2)/2] + o(\varepsilon)$  and  $\varepsilon\sigma^2 = \text{Var}[\ln \rho(t)] = \varepsilon[\sigma_1^2 + \sigma_2^2 - 2\theta_{12}] + o(\varepsilon)$ . Letting  $\mu = \mu_1 - \mu_2 + (\sigma_2^2 - \sigma_1^2)/2$  and  $\sigma^2 = \sigma_1^2 + \sigma_2^2 - 2\theta_{12}$ , we get the infinitesimal coefficients given in (5) and (6). A similar argument can be put forth for the case of variable adult death rates.

### CONCLUSION

The diffusion approximation that we have derived for the lottery model appears to provide a good approximation to the behavior of the original discrete-time lottery model over a broad range of conditions, but performs best when the population parameters in the model have lognormal distributions. This approximation has allowed us to obtain simple formulae giving conditions for coexistence and the stationary density, which permit the predictions of the model to be understood more easily. Especially

important is the observation that the adult death rates are the primary determinants of the population fluctuations of the coexisting species. While the environmental variance is critical to coexistence, its effect on population fluctuations, once coexistence has been achieved, is much less important than the adult death rates. In some ways this is not surprising because environmental variation has a dual role in the model. As shown in other work (e.g., Chesson and Warner, 1981), environmental variation leads to positive mean instantaneous growth rates at low density, which means that positive growth away from the boundaries toward the mean population density is promoted by environmental variability. But it is also clear that environmental variation should tend to cause a population near the mean to be pushed away from the mean. Thus environmental variability has two opposing tendencies in this model (Eqs. 7 and 8), and the results that we have obtained here suggest that these two opposing tendencies of environmental variation come to an equilibrium as environmental variability is increased.

As emphasized by Chesson (1986, 1988), coexistence in a stochastic environment results from an interaction between environmental variability and competitive factors. This interaction is caused here by the particular kinds of life-history traits that the organisms have. The life-history traits of relevance in the lottery model are that the organisms have overlapping generations and that competition occurs at the juvenile stage, which is also a stage that is sensitive to environmental fluctuations (through variability in the  $\beta$ 's). The overlap in generations can be measured quantitatively as  $1/d_i$ , which is essentially the mean longevity of adults. We have seen that this quantity involving life-history traits is most important in determining the stationary distribution and therefore the magnitude of the population fluctuations. Given that many properties of the lottery model have proved generalizable to other models (Chesson, 1986), it seems a reasonable conjecture that life-history features may well be the major determinants of population fluctuations in general stochastic environment models in which environmental variability promotes coexistence.

#### APPENDIX

##### *Diffusion Coefficients*

We have defined  $\rho(t) = \beta_1(t) \delta_2(t) / \beta_2(t) \delta_1(t) = e^{X(t)}$  and assumed  $E[X(t)] = \varepsilon\mu$ ,  $\text{Var}[X(t)] = \varepsilon\sigma^2$ ,  $\delta_i(t) = d_i e^{Y_i(t)}$ ,  $E[Y_i(t)] = 0$ ,  $i = 1, 2$ ,  $\text{Cov}[Y_1(t), X(t)] = \varepsilon\theta_1$ , and  $\text{Cov}[Y_2(t), -X(t)] = \varepsilon\theta_2$ . Note that  $X$ ,  $Y_1$ , and  $Y_2$  are of the form  $X = \varepsilon\mu + \sqrt{\varepsilon} V$ ,  $Y_1 = \sqrt{\varepsilon} V_1$ , and  $Y_2 = \sqrt{\varepsilon} V_2$ , with the  $V$ 's having mean zero and appropriate variances and covariance (e.g.  $\text{Var}(V) = \sigma^2$ ). In the following derivation, it will be necessary to have con-

vergence in mean to  $o(\varepsilon)$  of functions of  $X$ ,  $Y_1$ , and  $Y_2$  which are  $O_p(\varepsilon^{3/2})$  terms, and thus we must assume regularity conditions which allow us to conclude that  $E[O_p(\varepsilon^{3/2})] = O(\varepsilon^{3/2}) = o(\varepsilon)$ . For example, assuming that  $V$ ,  $V_1$ , and  $V_2$  are bounded random variables is one such set of conditions. To see this, suppose that  $f(X) = \sum_{n=1}^{\infty} (\varepsilon^{1/2})^n a_n(V)$  is a continuous function of  $V$ . Now, to approximate  $f(X)$ , note that  $f(X) = \sum_{n=1}^m (\varepsilon^{1/2})^n a_n(V) + O_p(\varepsilon^{(m+1)/2})$  and  $E[O_p(\varepsilon^{(m+1)/2})]$  does not necessarily equal  $O(\varepsilon^{(m+1)/2})$  unless  $V$  is a bounded random variable. We are not seeking the most general conditions under which the moment approximations hold, but only to verify that they at least apply to a broad class of situations. Thus, assume that  $E[O_p(\varepsilon^{(m+1)/2})] = O(\varepsilon^{(m+1)/2})$  with  $m=2$  in the derivation which follows. Substitution of the above assumptions and definitions into the lottery model yields

$$\begin{aligned} \Delta P_1 &= P_1(t + \varepsilon) - P_1(t) = P_1(t) P_2(t) \left\{ \frac{\beta_1(t) \delta_2(t) - \beta_2(t) \delta_1(t)}{\beta_1(t) P_1(t) + \beta_2(t) P_2(t)} \right\} \\ &= d_1 d_2 P_1(t) P_2(t) \left\{ \frac{\exp[X(t)] - 1}{d_1 P_1(t) \exp[X(t) - Y_2(t)] + d_2 P_2(t) \exp[-Y_1(t)]} \right\}. \end{aligned} \tag{A1}$$

Using power series expansions for  $e^{X(t)}$ ,  $e^{-Y_1(t)}$ ,  $e^{-Y_2(t)}$  and taking expected values gives

$$\begin{aligned} E[\Delta P_1 | P_1(t) = x] &= \frac{\varepsilon d_1 d_2 x(1-x)}{[d_1 x + d_2(1-x)]^2} \{ d_2 [\mu + \theta_1 + \sigma^2/2] \\ &\quad + [(d_1 - d_2)\mu - d_1 \theta_2 - d_2 \theta_1 - (d_1 + d_2)\sigma^2/2] x \} + o(\varepsilon) \\ &= \frac{\varepsilon d_1 d_2 x(1-x)}{[d_1 x + d_2(1-x)]^2} \{ d_1 x [\mu - \theta_2 - \sigma^2/2] \\ &\quad + d_2(1-x) [\mu + \theta_1 + \sigma^2/2] \} + o(\varepsilon) \end{aligned} \tag{A2}$$

and

$$E[\Delta P_1^2 | P_1(t) = x] = \frac{\varepsilon [d_1 d_2 \sigma x(1-x)]^2}{[d_1 x + d_2(1-x)]^2} + o(\varepsilon). \tag{A3}$$

Therefore,

$$\begin{aligned} \mu(x) &= \lim_{\varepsilon \downarrow 0} \frac{1}{\varepsilon} E[P_1(t + \varepsilon) - P_1(t) | P_1(t) = x] \\ &= \frac{d_1 d_2 x(1-x)}{[d_1 x + d_2(1-x)]^2} \{ d_1 x [\mu - \theta_2 - \sigma^2/2] + d_2(1-x) [\mu + \theta_1 + \sigma^2/2] \} \end{aligned} \tag{A4}$$

and

$$\sigma^2(x) = \lim_{\varepsilon \downarrow 0} \frac{1}{\varepsilon} E[\{P_1(t + \varepsilon) - P_1(t)\}^2 | P_1(t) = x] = \frac{[d_1 d_2 \sigma x(1-x)]^2}{[d_1 x + d_2(1-x)]^2}. \tag{A5}$$

*Boundary Classification*

In order to classify the boundaries, it is necessary to determine the conditions under which certain integrals are finite (Karlin and Taylor, 1981). If  $\alpha_1 = -(\gamma_1 + 1)/d_1$ ,  $\alpha_2 = -(\gamma_2 + 1)/d_2$ ,  $\gamma_1 = 2(\mu + \theta_1)/\sigma^2$ ,  $\gamma_2 = 2(-\mu + \theta_2)/\sigma^2$ ,  $c_1$  and  $c_2$  are positive constants,  $\xi \in (0, 1)$  is arbitrary, then for the left boundary these integrals are

$$S(0, x] = \lim_{a \downarrow 0} \int_a^x s(y) dy, \tag{A6}$$

where

$$\begin{aligned} s(y) &= \exp \left[ - \int_{\xi}^y \{2\mu(x)/\sigma^2(x)\} dx \right] \\ &= c_1 y^{\alpha_1} (1-y)^{\alpha_2} \quad (\text{for the lottery model}), \end{aligned} \tag{A7}$$

$$M(0, x] = \lim_{a \downarrow 0} \int_a^x m(y) dy, \tag{A8}$$

where

$$\begin{aligned} m(y) &= [\sigma^2(y) s(y)]^{-1} \\ &= c_2 [d_1 y + d_2(1-y)]^2 y^{-(\alpha_1+2)} (1-y)^{-(\alpha_2+2)} \\ &\quad (\text{for the lottery model}), \end{aligned} \tag{A9}$$

$$\Sigma(0) = \int_0^x \left\{ \int_z^x m(y) dy \right\} s(z) dz, \tag{A10}$$

and

$$N(0) = \int_0^x \left\{ \int_z^x s(y) dy \right\} m(z) dz \tag{A11}$$

Now,  $S(0, x] < \infty$  when  $\alpha_1 > -1$ , which implies  $d_1 > \gamma_1 + 1$ . Otherwise,  $S(0, x] = \infty$ . Similarly,  $M(0, x] < \infty$  when  $-(\alpha_1 + 2) > -1$ , which implies  $d_1 < \gamma_1 + 1$ . Otherwise,  $M(0, x] = \infty$ . According to Karlin and Taylor (1981),  $S(0, x] = \infty \Rightarrow \Sigma(0) = \infty$  and  $M(0, x] = \infty \Rightarrow N(0) = \infty$ . Thus,

$\Sigma(0) = \infty$  when  $d_1 \leq \gamma_1 + 1$  and  $N(0) = \infty$  when  $d_1 \geq \gamma_1 + 1$ . After some algebra (Hatfield, 1986), it can also be shown that  $\Sigma(0) = \infty$  when  $d_1 > \gamma_1 + 1$  and  $N(0) = \infty$  when  $d_1 < \gamma_1 + 1$ . Using the boundary classification scheme in Karlin and Taylor (1981), the left boundary, 0, is a natural boundary because  $\Sigma(0) = N(0) = +\infty$  for all  $d_1 \in (0, 1)$ . Due to the symmetry of the process, the right boundary, 1, is also a natural boundary.

*Comparison of Coexistence Criteria*

The conditions given by Chesson and Warner (1981) are  $E[\delta_1(t)\{\rho(t) - 1\}] > 0$  and  $E[\delta_2(t)\{\rho^{-1}(t) - 1\}] > 0$ , where  $\rho(t) = \beta_1(t)\delta_2(t)/\beta_2(t)\delta_1(t)$ . Making the definitions that  $\rho(t) = e^{X(t)}$ ,  $E[X(t)] = \mu$ ,  $\text{Var}[X(t)] = \sigma^2$ ,  $\delta_i(t) = d_i e^{Y_i(t)}$ , where  $E[Y_i(t)] = 0$ ,  $\text{Cov}[Y_1(t), X(t)] = \theta_1$ , and  $\text{Cov}[Y_2(t), -X(t)] = \theta_2$ , and assuming that  $Y_i(t)$  and  $X(t)$  have normal distributions, then

$$\begin{aligned} E[\delta_1(t)\{\rho(t) - 1\}] &= E[\delta_1(t)e^{X(t)}] - E[\delta_1(t)] \\ &= d_1 E[e^{X(t) + Y_1(t)}] - d_1 E[e^{Y_1(t)}] \\ &= d_1 \exp\{E[X(t) + Y_1(t)] + \text{Var}[X(t) + Y_1(t)]/2\} \\ &\quad - d_1 \exp\{E[Y_1(t)] + \text{Var}[Y_1(t)]/2\} \\ &= d_1 \exp\{\mu + \theta_1 + \sigma^2/2\} \exp\{\text{Var}[Y_1(t)]/2\} \\ &\quad - d_1 \exp\{\text{Var}[Y_1(t)]/2\}. \end{aligned} \tag{A12}$$

Now,  $E[\delta_1(t)\{\rho(t) - 1\}] > 0$  implies  $\exp\{\mu + \theta_1 + \sigma^2/2\} > 1$ , giving the condition  $\sigma^2 > -2(\mu + \theta_1)$ . Similarly, for the condition  $E[\delta_2(t)\{\rho^{-1}(t) - 1\}] > 0$ , we get  $\sigma^2 > -2(-\mu + \theta_2)$ . Therefore, the coexistence criteria from Chesson and Warner (1981) become  $\sigma^2 > 2 \max[-(\mu + \theta_1), -(-\mu + \theta_2)]$ .

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