

Extinction Rates for Fluctuation-Induced Metastabilities: A Real-Space WKB Approach

David A. Kessler¹ and Nadav M. Shnerb¹

Received November 16, 2006; accepted February 22, 2007

Published Online: March 23, 2007

The extinction of a single species due to demographic stochasticity is analyzed. The discrete nature of the individual agents and the Poissonian noise related to the birth-death processes result in local extinction of a metastable population, as the system hits the absorbing state. The Fokker-Planck formulation of the problem fails to capture the statistics of large deviations from the metastable state, while approximations appropriate close to the absorbing state become, in general, invalid as the population becomes large. To connect these two regimes, a real space WKB method based on the master equation is presented, and is shown to yield an excellent approximation for the decay rate and the extreme events statistics all the way down to the absorbing state. The details of the underlying microscopic process, smeared out in a mean field treatment, are shown to be crucial for an exact determination of the extinction exponent. This general scheme is shown to reproduce the known results in the field, to yield new corollaries and to fit quite precisely the numerical solutions. Moreover it allows for systematic improvement via a series expansion where the small parameter is the inverse of the number of individuals in the metastable state.

Local extinction due to demographic stochasticity is a key issue in the analysis of persistence and viability of small populations.^(1–3) In particular, it allows ecologists to identify endangered species and to specify conservation policies, it dictates the appearance and disappearance of favored and neutral genetic mutations⁽⁴⁾ and is of importance in the determination of the critical population size needed to support an epidemic.⁽⁵⁾ As in most cases of rare and extreme events the important quantities to be measured and compared with the theory are the expected extinction time of the populations,⁽²⁾ and the probability distribution close to the absorbing state. Technically, however, the effect of demographic stochasticity has traditionally

¹Department of Physics, Bar-Ilan University, Ramat-Gan 52900, Israel; e-mail: kessler@dave.ph.biu.ac.il

been taken into account using some version of a Fokker-Planck equation, where the “diffusion coefficient” is a function of the population size.⁽²⁾

Recently, much interest has been focussed on the calculation of extinction rates for systems whose macroscopic dynamics exhibits a stable state which is nevertheless only metastable due to rare fluctuations which can drive the system to extinction.^(6–9) In particular, it has been realized that in general the Fokker-Planck (FP) expansion about the (meta-)stable state is incapable of predicting the extinction rate. This is due to the fact that the Fokker-Planck expansion, as we shall show, is only valid for up to $O(N^{2/3})$ fluctuations to the large, $O(N)$, number of particles in the metastable state. The FP approximation fails to correctly describe the very large fluctuations necessary to reach the absorbing state of zero particles. The FP treatment also smears out the microscopic differences between processes as it reflects a local analysis close to the metastable fixed point. In order to get the correct statistics for rare and extreme events one should base the estimate on the exact Master equation that describes the stochastic process, and to employ the method of extreme statistics, or more simply put, the WKB approximation, to solve the relevant master equation.

Elgart and Kamenev⁽⁶⁾ made an interesting observation in this context: using the Peliti-Doi^(11,12) technique to map the exact master equation into a “quantum mechanical” problem (Schroedinger-like equation in imaginary time with second quantized Hamiltonian) they were able to identify the classical trajectory that connects the metastable fixed point and the absorbing state. This identification allows them to calculate the classical (“geometrical optics”) action along this trajectory, a first approximation to the extinction time. Assaf and Meerson⁽⁹⁾ then suggested a general spectral method to improve beyond the Elgart-Kamenev results, employing the generating function formalism and using the Sturm-Liouville theory of linear differential operators.

In this paper, we will present a general scheme to deal with the local extinction problem, based on the time-independent “real space” WKB approximation (unlike Refs.^(6,9) who used a time-dependent momentum space presentation). The method presented is easy to use, its intuitive meaning is transparent, and its range of applicability covers, essentially, any single species problem.

This paper will be organized as follows: In the next section we exemplify the technique for what is perhaps *the* archetypical problem in this class, a logistic birth-death process of a single species. Beside its importance, the solution of this example demands the use of all the components of the technique—a Fokker-Planck solution applicable close to the metastable fixed point, a small n approximation close to the absorbing state and a WKB solution that encompasses the FP regime and connects to the small n region. This model, thus, serves also as a nice pedagogical introduction. The third section deals with a similar birth death process, but when the number of offspring at each birth event is two, as in the case of domain walls in magnetic systems. Here, a series of mathematical “miracles” occur, which

allow for a simple calculation of the extinction rate (for the case of an initial even number of particles) without recourse to the WKB method. In the fourth section the effect of a single agent death term is incorporated, and in the last section the marginal case of equal birth and death rates is analyzed. We then conclude with a summary and some final observations.

1. STOCHASTICITY, LOGISTIC GROWTH AND EXTINCTION

In this section we study the stochastic dynamics of a combination of two fundamental processes: particles giving birth to new particles at a rate α ; and pair annihilation at a rate β . In that case the average number of particles is about α/β . The full “physical optics” solution for both the probability distribution, P_n , of the metastable state and the extinction rate, in the limit where $\beta \ll \alpha$ is given, based on a WKB approximation for the exact master equation. We confirm our calculations by comparison to a direct numerical solution of the master equation.

The microscopic rules that govern this process are:



The exact master equation for P_n , the probability of having n particles, is

$$\dot{P}_n = \alpha [-nP_n + (n - 1)P_{n-1}] + \frac{\beta}{2} [-n(n - 1)P_n + (n + 2)(n + 1)P_{n+2}]
 \tag{2}$$

At the mean-field level the process is described by the reaction equation,

$$\dot{n} = \alpha n - \beta n(n - 1)
 \tag{3}$$

which has the stable solution $n = \alpha/\beta + 1$. Technically, this expression may be derived from the exact master Eq. (2) by calculating the time derivative of the average population $\langle \dot{n} \rangle \equiv \sum n \dot{P}_n$ and using the approximation $\langle n^2 \rangle = \langle n \rangle^2$. The stable solution becomes metastable due to the effect of stochasticity (in particular, all particles may annihilate each other and the system will be stuck in the absorbing state $P_0 = 1$). Our aim is to calculate the typical time of this extinction event.

Since the stochastic process has no memory (a Markov process) it may be described by a transition matrix that specify the rates to pass from one microscopic configuration to the other. Clearly, the absorbing state $\{P_0 = 1, P_n = 0 \forall n \neq 0\}$ is an eigenvector of that matrix with an eigenvalue 0. All other eigenstates admit negative eigenvalues, and we denote the absolute value of the highest of these eigenvalues as Γ . The corresponding eigenvector is the stochastic metastable state, so our mission is to calculate Γ . Our main interest is in the case $\alpha/\beta \gg 1$ so that the typical number of particles is large. This implies that the probability to reach the absorbing state is, as we will calculate, exponentially small.

The metastability of the system implies that at long times the P_n decay exponentially as $e^{-\Gamma t}$. Thus we need to solve the master equation with the left-hand side replaced by $-\Gamma P_n$. However, since Γ is exponentially small, we can drop this term altogether. Technically this implies that we only have to solve for a steady state vector rather than doing time dependent semiclassical analysis which is much more complicated.

1.1. Fokker-Planck Equation and Its Limitations

The standard approach for solving the now time-independent master equation is to transform it into a Fokker-Planck (FP) equation^(1,3) The nominal prescription for doing this is to expand $P_{n\pm 1}$, etc. in a Taylor series, dropping terms involving more than two derivatives. However, phrasing the problem this way does not explain why, or more specifically, when this procedure is justified; moreover, the emerging equation is not unique—the same expansion may be done for $n P_n$, for example, yielding a different equation. The real justification underlying the Fokker-Planck approximation, as pointed out by van Kampen⁽¹³⁾ in his discussion of the Omega expansion, is that, for small β/α , P_n is a smooth function of the $O(1)$ variable

$$y \equiv \left(\frac{\beta}{\alpha}\right)^{1/2} \left(n - \frac{\alpha}{\beta}\right) \tag{4}$$

Then, $P_{n\pm 1}$ is equal to $P(y \pm \sqrt{\beta/\alpha})$ and so may be expanded formally with regard to the small parameter β/α . The resulting series may be written as:

$$\alpha \left[\hat{\mathcal{L}}_0 P(y) + \sqrt{\frac{\beta}{\alpha}} \hat{\mathcal{L}}_1 P(y) + \mathcal{O}\left(\frac{\beta}{\alpha}\right) + \dots \right] = 0 \tag{5}$$

where

$$\hat{\mathcal{L}}_0 P(y) = \left(\frac{d}{dy} (yP) + \frac{3}{2} \frac{d^2}{dy^2} P \right) \tag{6}$$

and

$$\hat{\mathcal{L}}_1 P(y) = \frac{1}{2} (P''' + 5yP'' + 8P' + 4yP + 2y^2P) \tag{7}$$

This perturbative expansion is justified (at least in the sense of asymptotic series) if, expanding $P(y) = P_0(y) + \sqrt{\beta/\alpha} P_1(y) + \dots$, the correction term $\sqrt{\beta/\alpha} P_1(y) \ll P_0(y)$. Plugging this series into (5) and collecting terms order by order one finds that

$$P_0(y) = C e^{-y^2/3} = C e^{-\beta(n-\alpha/\beta)^2/3\alpha}. \tag{8}$$

Then, looking at the equation for P_1

$$\hat{\mathcal{L}}_0 P_1(y) = -\sqrt{\frac{\beta}{\alpha}} \hat{\mathcal{L}}_1 P_0(y), \tag{9}$$

one is able to identify that the leading correction is proportional to $y^3 \sqrt{\beta/\alpha} P_0(y)$. Thus the the FP equation is only valid up to $(n - \alpha/\beta) \sim (\alpha/\beta)^{2/3}$, as mentioned above. This limit on the FP reliability is clearly demonstrated in Fig. 1, where the FP solution is compared to an exact numerical solution of the time-independent master equation. We see that for a metastable population of 100 individuals, the FP solution is a good approximation to the exact probability distribution only for n 's between 70 and 130. We note in passing that this limitation of the FP solution is not apparent in van Kampen's discussion, as van Kampen only studies the corrections to the moments of the distribution, which are determined to all orders by the neighborhood of the Gaussian peak, and not the corrections to the distribution itself. Of course, the failure of the FP solution away from the peak is responsible for the Omega expansion only being an asymptotic, rather than convergent, expansion.

To find the decay rate, however, we need to have a solution valid down to $n = 1$, and the FP solution does not suffice. Our next step then is to consider the low n limit of the master equation.

1.2. Probability Distribution Close to Extinction

In the vicinity of the absorbing state one may use a simplified form of the master equation, exploiting the fact that P_n is a rapidly growing function of n . Then, $P_n \ll P_{n+2}$ and $P_{n-1} \ll P_n$, yielding the simplified recursion relation:

$$P_{n+2} = \left(\frac{2\alpha}{\beta}\right) \frac{n}{(n+2)(n+1)} P_n \tag{10}$$

This approximate recursion relation leaves the even and odd n 's decoupled, and has the solution

$$\begin{aligned} P_{2k} &= \left(\frac{4\alpha}{\beta}\right)^{k-1} \frac{2(k-1)!}{(2k)!} P_2 \\ P_{2k+1} &= \left(\frac{\alpha}{\beta}\right)^k \frac{1}{(2k+1)k!} P_1 \end{aligned} \tag{11}$$

with P_1, P_2 arbitrary. Examining Eq. (10), we see that if $P_1 \ll P_2$, then as long as $n \ll \alpha/\beta$, our assumption leading to the approximate recursion relation is valid. It is also clear that the rapid rise of the P_n 's slows as n increases, with the P_n 's reaching a maximum at $n = 2\alpha/\beta$. Clearly, however, the maximum probability state is at $n \approx \alpha/\beta$, so the recursion relation must fail before the bulk regime. In fact, our recursion relation works up to $\beta n/\alpha \ll 1$ whereas the FP solution only works when $\beta n/\alpha \approx 1$. There is no way to directly connect these two regimes. This is seen clearly in Fig. 1, where the recursion relation and FP solutions are shown for the case $\beta/\alpha = 0.01$. The resolution to this problem lies in the WKB

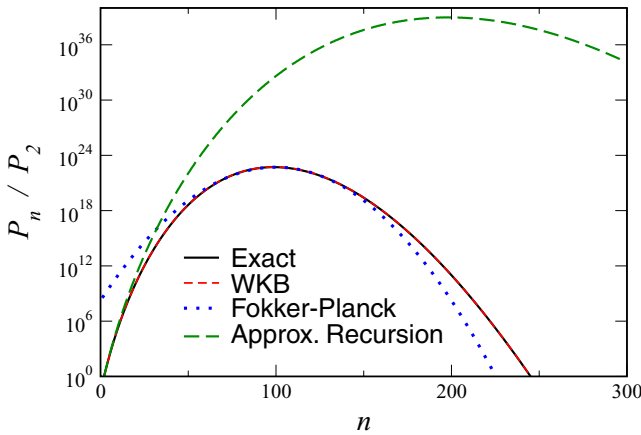


Fig. 1. (color online) Probability distribution P_n/P_2 for $\beta = 0.01$, $\alpha = 1$, for the basic model, Eq. (1), (obtained from a direct numerical solution of the master equation, Eq. (2)) together with the WKB approximation, Eq. (30) along with Eqs. (16), (29), and (32); the FP approximation, Eq. (33); and the low/intermediate- n result, Eq. (11). Note that on the scale of the figure, the WKB approximation is indistinguishable from the exact result.

method, which will allow us to connect the recursion relation results to the FP regime.

1.3. WKB Approximation and the Extinction Rate—The Leading Term

To do WKB for our difference equation,⁽¹⁴⁾ we write $P_n = e^{S_n}$, where S_n is assumed to be a smooth function of n , so that $S_{n\pm 1} \approx S_n \pm S'_n$. Since we already know (from the FP treatment) that the probability profile in the bulk is a Gaussian with width proportional to the square root of the metastable population, the quality of this approximation is controlled. Writing $\Lambda_n \equiv e^{S'_n}$, we have, assuming $n \gg 1$,

$$0 = \alpha \left(-n + \frac{n}{\Lambda_n} \right) + \frac{\beta}{2} (-n^2 + n^2 \Lambda_n^2) \tag{12}$$

or, simplifying,

$$\begin{aligned} 0 &= \beta n \Lambda_n^3 - (2\alpha + \beta n) \Lambda_n + 2\alpha \\ &= (\Lambda_n - 1)(\beta n \Lambda_n^2 + \beta n \Lambda_n - 2\alpha) \end{aligned} \tag{13}$$

where we have factored out the trivial $\Lambda_n = 1$ root which is a result of conservation of probability. The other two roots for Λ are

$$\Lambda_n = -\frac{1}{2} \pm \frac{\sqrt{1 + \frac{8\alpha}{\beta n}}}{2}, \tag{14}$$

of which the larger, positive, one is relevant for us, since we want P_n to be an increasing function. This implies that

$$S'_n = \ln \left(\frac{\sqrt{1 + \frac{8\alpha}{\beta n}} - 1}{2} \right) \tag{15}$$

Integrating, we find that

$$\begin{aligned} S_n = S_0 + n \ln \left(\sqrt{1 + \frac{8\alpha}{\beta n}} - 1 \right) + \frac{1}{2} n \sqrt{1 + \frac{8\alpha}{\beta n}} \\ - \frac{2\alpha}{\beta} \ln \left(\frac{\beta n}{4\alpha} + 1 + \frac{\beta n}{4\alpha} \sqrt{1 + \frac{8\alpha}{\beta n}} \right) - n \ln(2) + \frac{1}{2} n \end{aligned} \tag{16}$$

The first important point to notice is that $\alpha/(\beta n)$ extrapolates, in the interesting region, from ∞ as $n \rightarrow 0$ to unity, where $n \rightarrow \alpha/\beta$. In the first case S' scales logarithmically with $\alpha/(\beta n)$, hence S_n is proportional to $\alpha/(\beta n)$ and is large. In the second regime S' is almost constant and S_n scales with n which is also, in that case, large. Thus all the way to extinction S_n is large, as expected. Evaluating $\Delta S \equiv S_{\alpha/\beta} - S_0$, one obtains

$$\Delta S = \frac{2\alpha}{\beta} (1 - \ln(2)) \tag{17}$$

in agreement with the result of Elgart and Kamenev.⁽⁶⁾

We can make the connection to the formalism presented in Ref.⁽⁶⁾ even more explicit, if we express the relations in terms of $n(\Lambda)$ as opposed to Λ_n . From Eq. (13),

$$n(\Lambda) = \frac{2\alpha}{\beta \Lambda (\Lambda + 1)} \tag{18}$$

thus

$$\begin{aligned} \Delta S &= \int_0^{\alpha/\beta} \ln(\Lambda_n) dn \\ &= - \int_1^\infty \ln(\Lambda) \frac{dn}{d\Lambda} d\Lambda \end{aligned}$$

$$\begin{aligned}
 &= -\ln(\Lambda)n(\Lambda)|_1^\infty + \int_1^\infty \frac{n(\Lambda)}{\Lambda} d\Lambda \\
 &= \int_1^\infty \frac{n(\Lambda)}{\Lambda} d\Lambda.
 \end{aligned} \tag{19}$$

If we now introduce the “momentum” $p \equiv 1/\Lambda$ and the “coordinate” $q \equiv n\Lambda$, the expression for ΔS may be rewritten as

$$\Delta S = \int_0^1 q dp \tag{20}$$

where

$$q(p) = \frac{2\alpha}{\beta} \frac{p}{1+p} \tag{21}$$

precisely reproducing the Elgart-Kamenev equations for the action and the semiclassical escape path. The physical meaning of the “momentum” p is now clarified: it is the inverse of the geometrical growth rate of the quasistatic probability distribution.

We now need to confirm that there exists an overlap region between the WKB solution and the $n \ll \alpha/\beta$ recursion regime. For $n \ll \alpha/\beta$ our WKB solution for S_n may be approximated by,

$$S_n \approx S_0 + \frac{1}{2}n \left(1 + \ln \left(\frac{2\alpha}{\beta n} \right) \right) \tag{22}$$

To compare this with the recursion relation results, Eq. (11), in the limit $n \gg 1$:

$$\begin{aligned}
 \ln(P_n^{even}) &\approx \frac{1}{2}n \left(1 + \ln \left(\frac{2\alpha}{\beta n} \right) \right) + \frac{3}{2} \ln(2) - \ln \left(\frac{4\alpha n}{\beta} \right) + \ln(P_2) \\
 \ln(P_n^{odd}) &\approx \frac{1}{2}n \left(1 + \ln \left(\frac{2\alpha}{\beta n} \right) \right) - \frac{1}{2} \ln \left(\frac{2\pi\alpha n^2}{\beta} \right) + \ln(P_1)
 \end{aligned} \tag{23}$$

Indeed, the leading order asymptotics agrees.

In the other extreme our WKB result coincides with the FP treatment. Expanding the WKB solution for small $y \equiv \sqrt{\beta/\alpha}(n - \alpha/\beta)$ yields

$$\ln(S_n) = \ln(\Delta S - y^2/3) \tag{24}$$

reproducing the FP solution.

1.4. WKB Approximation and the Extinction Rate—First Order Corrections

The explicit real space, time-independent WKB analysis allows one to go beyond the Elgart-Kamenev “geometrical optics” results and to obtain the leading

corrections. In the previous subsection the generic substitution $P_n = \exp(S_n)$ was implemented and is justified *ex post facto* by the fact that S_n turns out to be $\mathcal{O}(\alpha/\beta) \gg 1$. To proceed let us assume that

$$P_n = \exp(S_0(n) + S_1(n) + S_2(n) + \dots) \tag{25}$$

where $S_0(n)$ is the leading order S_n found above and $S_m(n)$ is assumed to be $\mathcal{O}((\beta/\alpha)^{m-1})$. Beginning with the growth part of the master equation $T_\alpha \equiv \alpha[-nP_n + (n-1)P_{n-1}]$, plugging in Eq. (25) and expanding the small ($\mathcal{O}(\beta/\alpha)$) terms in the exponent one has (note that any derivative adds a (β/α) factor):

$$\begin{aligned} T_\alpha &= \alpha e^{S_0(n)+S_1(n)+S_2(n)} \left(-n + (n-1)e^{-S_0(n)} \left[1 + \frac{1}{2}S_0'' - S_1' \right] \right) \\ &= \alpha n e^{S_0+S_1+S_2} \left[\left(-1 + \frac{1}{\Lambda_n} \right) + \frac{1}{\Lambda_n} \left(\frac{S_0''}{2} - S' - \frac{1}{n} \right) \right] \end{aligned} \tag{26}$$

While the first, $\mathcal{O}(1)$, term in the bracket was used to determine Λ , the second $\mathcal{O}(\beta/\alpha)$ term will be used here in order to find the function S_1 . Repeating that procedure and collecting the leading corrections from the annihilation part of the Master equation one finds,

$$0 = \frac{\alpha}{\Lambda_n} \left(-S_1' + \frac{S_0''}{2} - \frac{1}{n} \right) + \frac{\beta n}{2} \left(\frac{1}{n} + 2\Lambda_n^2 S_1' + 2\Lambda_n^2 S_0'' + \frac{3}{n} \Lambda_n^2 \right) \tag{27}$$

Things simplify if we write S_1 as a function of Λ :

$$\left[\frac{\alpha}{\Lambda} - \beta n \Lambda^2 \right] \frac{d}{d\Lambda} S_1 = \frac{1}{2\Lambda} \left[\frac{\alpha}{\Lambda} + 2\beta n \Lambda^2 \right] + \frac{n'(\Lambda)}{2n} \left[-\frac{2\alpha}{\Lambda} + \beta n + 3\beta n \Lambda^2 \right] \tag{28}$$

so that all the coefficient functions are rational functions of Λ . The solution of this equation is best expressed in terms of $Q_n \equiv e^{S_1(n)}$:

$$Q_n = A \frac{\sqrt{\Lambda_n}(\Lambda_n + 1)^2}{\sqrt{2\Lambda_n + 1}} \tag{29}$$

so that to this order

$$P_n \approx Q_n e^{S_n} \tag{30}$$

We see that Q_n diverges as n^{-1} as $n \rightarrow 0$, since Λ_n diverges there, and vanishes as $n^{-1/2}$ for large n , where Λ vanishes. Interestingly enough, there is no turning point, and the WKB approximation is good everywhere. This holds despite the fact that the coefficient of Q_n' vanishes at $\Lambda = 1$, where S' vanishes, as is typical for WKB problems. In our case, the right hand side also vanishes at $\Lambda = 1$, so Q is regular there. We suspect that this is a consequence of the effective vanishing

of Γ , so that the FP equation admits a trivial first integral, and so is effectively of first order.

With this result for Q_n in hand, we can finish the matching procedure. For $n \ll \alpha/\beta$, Λ_n is large as we noted, and

$$Q_n \approx A \frac{\sqrt{2}\alpha}{\beta n} \quad (31)$$

Comparing to the recursion relation results, we have

$$\begin{aligned} A &= P_2 \frac{\beta^2}{2\alpha^2} \\ &= P_1 \sqrt{\frac{\beta^3}{4\pi\alpha^3}} \end{aligned} \quad (32)$$

This fixes the ratio of P_1 to P_2 , which is precisely that which makes $\ln(P_n)$ a smooth function. About the maximum, $\Lambda_n \approx 1$, so that $Q_n \approx 4A/\sqrt{3}$, and

$$P_n \approx \frac{2}{\sqrt{3}} \left(\frac{\beta}{\alpha}\right)^2 P_2 e^{\Delta S} e^{-y^2/3} \quad (33)$$

The sum over P_n is dominated by this FP Gaussian, and so, replacing the sum by an integral, we get

$$P_{\text{tot}} \approx 2\sqrt{\pi} \left(\frac{\beta}{\alpha}\right)^{3/2} P_2 e^{\Delta S} \quad (34)$$

The decay rate Γ is then

$$\Gamma = \beta \frac{P_2}{P_{\text{tot}}} \approx \sqrt{\frac{\alpha^3}{4\pi\beta}} e^{-2\alpha(1-\ln(2))/\beta} \quad (35)$$

Note that the normalization of the P_n 's is not necessary, since all the P_n 's scale with P_2 , and so the normalization factor cancels in the calculation of Γ . Our result for Γ is plotted in Fig. 2, where we see the agreement is excellent for small β . As Γ varies by so many orders of magnitude over the scale of the graph, it is impossible to see from this the role of the prefactor. In Fig. 3, we plot the ratio of Γ to $e^{\Delta S}$ as a function of β . We see the accuracy is quite good and gets better as β gets smaller, as expected. This prefactor is, it should be noted, quite different from the factor α conjectured in Ref. (6). In Fig. 1, we present the graph of P_n together with the WKB, Fokker-Planck, and low/intermediate n approximations. We see that the WKB approximation is excellent everywhere, whereas the other approximations are more limited in their range of validity. In particular, the Fokker-Planck results is a serious overestimate of the low n probability, and an equally bad underestimate of the large n probability. As the WKB and exact results cannot be distinguished

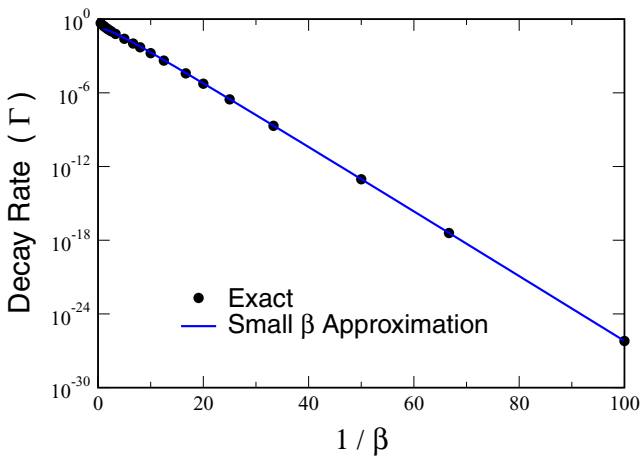


Fig. 2. (color online) Decay rate Γ vs. $1/\beta$, for the basic model, Eq. (1), with $\alpha = 1$, together with the analytic approximation, Eq. (35). Here and in all other figures, the numerical calculation of the decay rate was performed using a quadruple-precision version of the sparse matrix eigenvalue solver ARPACK,⁽¹⁵⁾ applied to the master equation transition matrix, with the absorbing state eliminated.

on the scale of the figure, in Fig. 4 we present the ratio of the WKB to the exact result for $\alpha = 1, \beta = 0.01$. We see that the WKB approximation is good to the expected few percent level, with it degrading slightly for very small n . Given that the WKB approximation is a large- n approximation, that it does as well as it does at low- n is an undeserved present, and a consequence of the remarkable accuracy of Stirling’s formula down to $n = 1$.

For completeness, we note that it is possible to derive a large β expansion of Γ as well. This is easily done by truncating the master equation matrix and computing its determinant as a power series in α/β , then solving for Γ order by order. One finds

$$\Gamma \approx \alpha - 2 \frac{\alpha^2}{\beta} + \frac{10}{3} \frac{\alpha^3}{\beta^2} - \frac{38}{9} \frac{\alpha^4}{\beta^3} + \frac{242}{135} \frac{\alpha^5}{\beta^4} \tag{36}$$

It seems clear that this series has at best a finite radius of convergence. Both large and small β limits are compared to the exact results in Fig. 5.

2. PARITY-PRESERVING MODEL

In this section we will discuss the case where birth is to “twins”, so that the even-odd parity of the number of particles is preserved. Here, a series of mathematical “miracles” occur, which allow for a simple calculation of the extinction rate (for the case of an initial even number of particles) without recourse to the

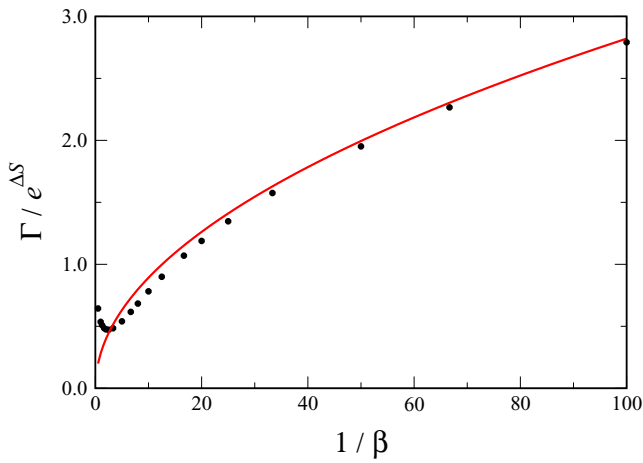


Fig. 3. (color online) Ratio of Γ to $e^{\Delta S}$, for the basic model, Eq. (1), compared to the WKB prediction, as a function of β , for $\alpha = 1$.

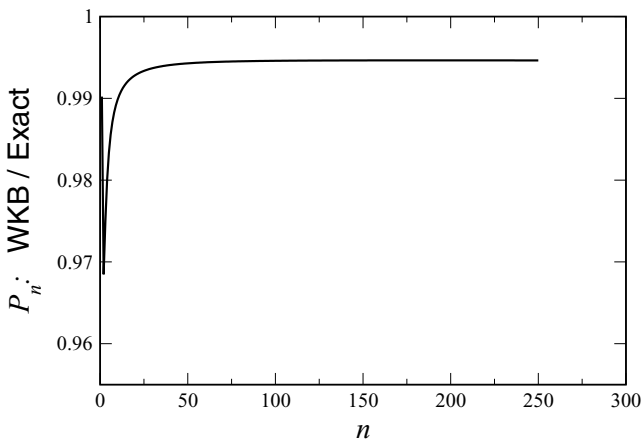


Fig. 4. Ratio of the WKB approximation for P_n to the exact result for the basic model, Eq. (1) for $\beta = 0.01$, $\alpha = 1$.

WKB method. Furthermore, we present a solution of the probability distribution to *all* orders in β/α , so that the corrections are exponentially small. We also calculate the extinction rate to all orders in perturbation theory and manage to resum this divergent asymptotic series to obtain results correct to within exponentially small terms.

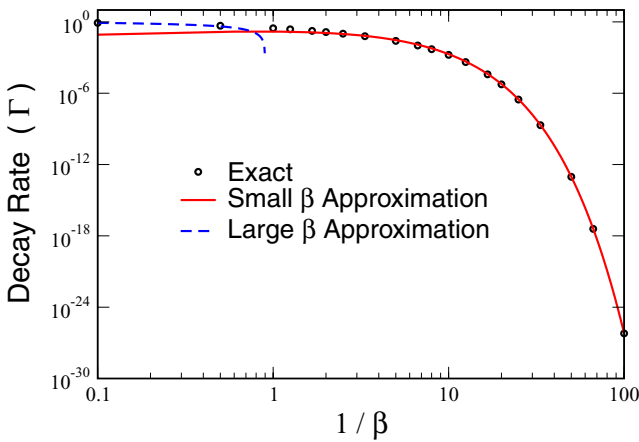


Fig. 5. (color online) Decay rate Γ vs. $1/\beta$ for the basic model, Eq. (1), with $\alpha = 1$, together with the large β approximation, Eq. (36), and the small β approximation, Eq. (35).

The model,



conserves the even/odd parity of the number of particles, so if the system is initialized with an odd number of particles it can never go extinct, instead reaching a steady-state. If the system is initialized with an even number of particles, on the other hand, the system can go extinct, with the survival probability decaying again as $e^{-\Gamma t}$, with Γ exponentially small for small β . It should be noted that the mean-field equation for the model is the exact same as that of the original model above.

We again start with the master equation, which now reads:

$$\begin{aligned}
 \dot{P}_n = -\Gamma P_n = &\frac{\alpha}{2}[-nP_n + (n-2)P_{n-2}] \\
 &+ \frac{\beta}{2}[-n(n-1)P_n + (n+2)(n+1)P_{n+2}]
 \end{aligned}
 \tag{38}$$

As above, Γ is exponentially small, and we may drop this term altogether. We again tackle the master equation by exploiting the fast growth of the P_n 's for not too large n . This observation allows us to drop the second α term and the first β term, yielding the recursion relation

$$P_{n+2} = \left(\frac{\alpha}{\beta}\right) \frac{n}{(n+1)(n+2)} P_n
 \tag{39}$$

which, up to a factor of 2, is the same as the approximate recursion relation we previously encountered. Now, however, the parity conservation implies that only the even terms are nonzero, with the odd terms being exactly decoupled. The recursion relation has the solution

$$P_{2k} = \left(\frac{\alpha}{\beta}\right)^{k-1} \frac{(k-1)!2^k}{(2k)!} P_2 \quad (40)$$

In principle, we should have to match this solution to the WKB solution, as we did in the nonparity case. The first miracle we encounter is that in fact the solution Eq. (40) is accurate throughout the Fokker-Planck region. To see this, note that for $n = \alpha/\beta + y\sqrt{\alpha/\beta}$, $y \sim O(1)$, the asymptotic expansion of P_n is

$$P_n \approx \sqrt{2} \left(\frac{\beta}{\alpha}\right)^2 e^{\alpha/2\beta} P_2 e^{-y^2/4} \quad (41)$$

It is straightforward to verify that this is the solution of the Fokker-Planck equation:

$$0 = \alpha \left(\frac{d}{dy} (yP) + 2 \frac{d^2}{dy^2} P \right) \quad (42)$$

It should be noted for the record that while Eq. (40) is an accurate representation of P_n from $n = 2$ till past the peak, the Fokker-Planck Gaussian is again only valid in the peak region.

Thus, we can use Eq. (40) to calculate $P_{\text{tot}} \equiv \sum_k P_{2k}$. We find

$$P_{\text{tot}} \approx P_2 \sum_{k=1}^{\infty} \left(\frac{\alpha}{\beta}\right)^{k-1} \frac{(k-1)!2^k}{(2k)!} = {}_2F_2\left(1, 1; \frac{3}{2}, 2; \frac{\alpha}{2\beta}\right) P_2 \quad (43)$$

For the moment, what is important is the leading order asymptotics of this, which can be calculated directly by applying Laplace's method to the sum. This is equivalent to integrating the Gaussian, and gives

$$P_{\text{tot}} \approx \sqrt{2\pi} \left(\frac{\beta}{\alpha}\right)^{3/2} e^{\alpha/2\beta} P_2 \quad (44)$$

We are essentially done. The rate of probability flux out to the absorbing state is βP_2 , which equals ΓP_{tot} . Thus,

$$\Gamma = \frac{\beta P_2}{P_{\text{tot}}} \approx \frac{\beta}{\sqrt{2\pi} \left(\frac{\beta}{\alpha}\right)^{3/2} e^{\alpha/2\beta}} = \sqrt{\frac{\alpha^3}{2\pi\beta}} e^{-\alpha/2\beta} \quad (45)$$

Note again that this is much smaller than the naive Fokker-Planck answer, which is proportional to $e^{-\alpha/4\beta}$.

We can actually proceed to compute the corrections to this formula. One source of corrections is using the asymptotics of ${}_2F_2$. The full asymptotics of ${}_2F_2$

for large argument are very beautiful:

$${}_2F_2\left(1, 1; \frac{3}{2}, 2; x\right) \approx \sqrt{\frac{\pi}{4x^3}} e^x \left(1 + \sum_{k=1}^{\infty} \frac{(2k-1)!!}{(2x)^k}\right) \tag{46}$$

This is obviously a divergent series, and alternatively represents a resummation of the series. This result is easily proven by substituting it in the Hypergeometric Differential Equation.

The second source of the corrections is the corrections to the P_n 's due to the terms we dropped in the master equation. The structure here is also strikingly beautiful. If we denote our zeroth-order approximation of P_n by P_n^0 , we find

$$\begin{aligned} P_4 &= P_4^0 \left(1 + \frac{\beta}{\alpha}\right) \\ P_6 &= P_6^0 \left(1 + \frac{\beta}{\alpha} + 3\left(\frac{\beta}{\alpha}\right)^2\right) \\ P_8 &= P_8^0 \left(1 + \frac{\beta}{\alpha} + 3\left(\frac{\beta}{\alpha}\right)^2 + 15\left(\frac{\beta}{\alpha}\right)^3\right) \end{aligned} \tag{47}$$

The general trend is obvious:

$$P_{2k} = P_{2k}^0 \left(1 + \sum_{m=1}^{k-1} (2m-1)!! \left(\frac{\beta}{\alpha}\right)^m\right) \tag{48}$$

Plugging this into the master equation shows that this is an exact solution (for $\Gamma = 0$, of course). Now, up to exponentially small corrections, P_{tot} is just multiplied by the correction factor:

$$\begin{aligned} P_{\text{tot}} &= P_{\text{tot}}^0 \left(1 + \sum_{m=1}^{\infty} (2m-1)!! \left(\frac{\beta}{\alpha}\right)^m\right) \\ &= P_{\text{tot}}^0 \sqrt{\frac{\alpha^3}{2\pi\beta^3}} e^{-\alpha/2\beta} {}_2F_2\left(1, 1; \frac{3}{2}, 2; \frac{\alpha}{2\beta}\right) \end{aligned} \tag{49}$$

The final result for Γ is

$$\Gamma \approx \frac{\sqrt{2\pi\beta^5/\alpha^3}}{\left[{}_2F_2\left(1, 1; \frac{3}{2}, 2; \frac{\alpha}{2\beta}\right)\right]^2} e^{\alpha/2\beta} \tag{50}$$

Even though this answer is a resummation of the full asymptotic series, it is nevertheless not exact. The correction terms however are exponentially small, (relative to the exponentially small extinction rate) going like $e^{-\alpha/\beta}$. This can be seen in the following graph, where we plot the relative error, comparing to

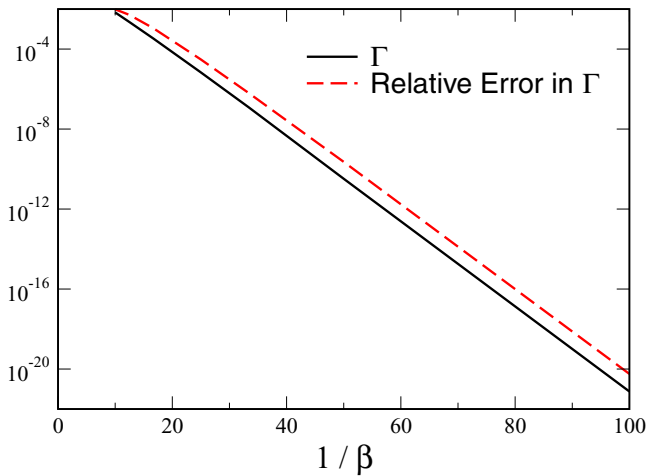


Fig. 6. (color online) Extinction rate Γ and the relative error between the approximation, Eq. (50), and the exact value as a function of $1/\beta$ for $\alpha = 1$.

an essentially exact numerical calculation (using extended precision arithmetic in Maple). Thus, for example, the error for $\alpha/\beta = 100$ is six parts in 10^{21} !

For completeness, we also briefly write down the WKB solution. Firstly,

$$n(\Lambda) = \frac{\alpha}{\beta\Lambda^2} \quad (51)$$

so that

$$\Delta S = \int_1^\infty \frac{n}{\Lambda} d\Lambda = \frac{\alpha}{2\beta} \quad (52)$$

Also,

$$S_n = \frac{n}{2} [\ln(\alpha/\beta) + 1 - \ln(n)] \quad (53)$$

The solution for Q_n is the simple result

$$Q_n = A\Lambda^2 \quad (54)$$

All this can be seen to agree with our recursion relation solution. In fact, it implies that the recursion relation solution is valid everywhere, even past the FP regime.

One can again calculate the large β limit of the decay rate. The first few terms of this series are:

$$\Gamma = \beta - \frac{\alpha}{5} + \frac{12\alpha^2}{875\beta} - \frac{4\alpha^3}{21875\beta^2} - \frac{972\alpha^4}{58953125\beta^3} + \frac{24964\alpha^5}{95798828125\beta^4} \quad (55)$$

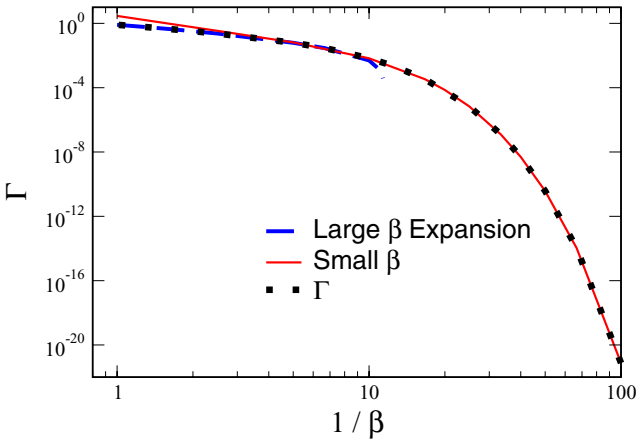


Fig. 7. (color online) Decay rate Γ for the parity conserving model, compared to the small β result, Eq. (50), and the large β power-series expansion, Eq. (55). The agreement between these analytical expressions and the exact results is so good in their respective spheres of validity, that the deviations are only visible quite far outside these areas.

It would appear likely that this series is actually convergent. In any case, together with the small β/α results above, they cover the entire range of parameters, as can be seen in Fig. 7.

3. GENERAL NONPARITY MODEL

Let us extend, now, our original, non-parity preserving, model to include a third process, the spontaneous death of particles at a rate $\gamma < \alpha$. Such a process appears naturally in many systems, from populations of animals (where γ is the death rate of an individual) to the spread of a disease (where it correspond to a recovery of an infected agent, like in the SIR model⁽⁵⁾). We present the physical optics solution for this case also, again confirming it by comparison to the direct numerical solution.

Adding the spontaneous decay of particles:

$$P \xrightarrow{\gamma} 0 \tag{56}$$

to our basic model, Eq. (1), changes both the mean field and the fluctuations. At the mean-field level this is equivalent to a simple change of α to an effective growth rate $\alpha_{eff} = \alpha - \gamma$, but this scaling is not true anymore if the fluctuations are taken into account. The master equation now reads:

$$\begin{aligned} \dot{P}_n = & \alpha [-nP_n + (n - 1)P_{n-1}] + \frac{\beta}{2} [-n(n - 1)P_n + (n + 2)(n + 1)P_{n+2}] \\ & + \gamma [-nP_n + (n + 1)P_{n+1}]. \end{aligned} \tag{57}$$

We start this time with the WKB solution. As before, the WKB ansatz yields an equation for Λ_n , namely

$$\begin{aligned} 0 &= \left(\frac{1}{2\Lambda_n}\right) [2\alpha(-\Lambda_n + 1) + \beta n(-\Lambda_n + \Lambda_n^3) + 2\gamma(-\Lambda_n + \Lambda_n^2)] \\ &= \left(\frac{\Lambda_n - 1}{2\Lambda_n}\right) [-2\alpha + \beta n\Lambda_n(\Lambda_n + 1) + 2\gamma\Lambda_n] \end{aligned} \quad (58)$$

with the solution

$$\Lambda_n = \frac{\sqrt{(\beta n + 2\gamma)^2 + 8\alpha\beta n} - 2\gamma - \beta n}{2\beta n} \quad (59)$$

Now, Λ approaches the finite limit, α/γ as n goes to 0, in contrast to the previous cases. Thus, we cannot solve the low- n recursion relation by assuming that the P_n are increasing very rapidly. Rather, now β is irrelevant for low n , and we have to solve the $\beta = 0$ recursion. This is readily solved, for example by generating function techniques, and yields

$$P_n = \frac{\gamma}{n(\alpha - \gamma)} \left[\left(\frac{\alpha}{\gamma}\right)^n - 1 \right] P_1 \quad (60)$$

Indeed, for large n P_n grows geometrically, with the ratio α/γ , agreeing with the small n WKB.

We can now proceed with the remainder of the WKB procedure. As before, it is more convenient to work with $n(\Lambda)$, given by

$$n(\Lambda) = \left(\frac{2}{\beta}\right) \frac{\alpha - \gamma\Lambda}{\Lambda(\Lambda + 1)} \quad (61)$$

We see that in the mean-field regime, $\Lambda \approx 1$, the entire γ dependence is through α_{eff} . Away from this limit, however, the situation is more complicated.

Now, as before, S_n is given by

$$\begin{aligned} S_n &= S_0 - [n(\Lambda) \ln(\Lambda)]_{\Lambda}^{\alpha/\gamma} + \int_{\Lambda}^{\alpha/\gamma} \frac{n(\Lambda)}{\Lambda} d\Lambda \\ &= S_0 + n \ln(\Lambda) + \frac{2(\alpha - \gamma\Lambda)}{\beta\Lambda} - \frac{2(\alpha + \gamma)}{\beta} \left(\ln\left(\frac{\Lambda + 1}{\Lambda}\right) - \ln\left(\frac{\alpha + \gamma}{\alpha}\right) \right) \end{aligned} \quad (62)$$

In particular,

$$\Delta S = \frac{2(\alpha - \gamma)}{\beta} + \frac{2(\alpha + \gamma)}{\beta} \ln\left(\frac{\alpha + \gamma}{2\alpha}\right) \quad (63)$$

We exhibit ΔS as a function of γ for fixed α in Fig. 8. We see that ΔS decreases with increasing γ , vanishing quadratically as γ approaches the threshold value of

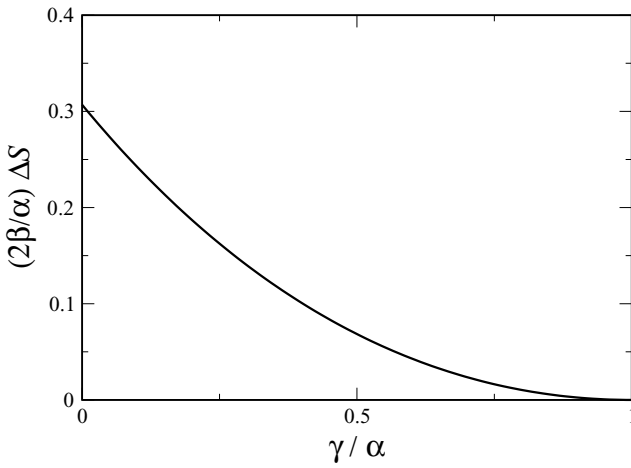


Fig. 8. $2\beta\Delta S/\alpha$ as a function of γ , for fixed α .

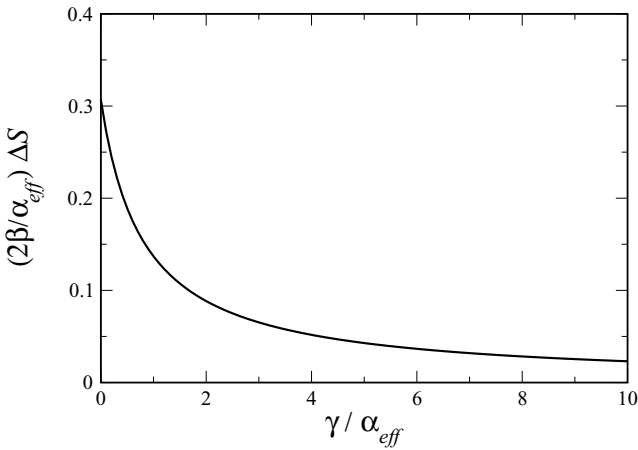


Fig. 9. $2\beta\Delta S/\alpha_{eff}$ as a function of γ , for fixed α_{eff} .

α . Also interesting is the dependence of ΔS as a function of γ , for fixed α_{eff} . This is shown in Fig. 9. We see that as γ increases, at fixed α_{eff} , ΔS decreases, leading to a faster decay rate due to increased fluctuations. For large γ , in fact, ΔS vanishes as $\alpha_{eff}/(2\beta\gamma)$.

We now are in a position to continue to the calculation of $Q_n = e^{S_1(n)}$. The equation is

$$\begin{aligned}
 0 = & \alpha \left[-n + \frac{n}{\Lambda_n} \left(1 - S'_1 + \frac{1}{2} S''_0 - \frac{1}{n} \right) \right] \\
 & + \frac{\beta}{2} \left[-n^2 + n + n^2 \Lambda_n^2 \left(1 + 2S'_1 + 2S''_0 + \frac{3}{n} \right) \right] \\
 & + \gamma \left[-n + n \Lambda_n \left(1 + S'_1 + \frac{1}{2} S''_0 + \frac{1}{n} \right) \right]
 \end{aligned} \tag{64}$$

which simplifies to, using $S'' = 1/(\Lambda n'(\Lambda))$,

$$\begin{aligned}
 & \left[\frac{\alpha}{\Lambda} - \beta n \Lambda^2 - \gamma \Lambda \right] \frac{d}{d\Lambda} S_1 \\
 = & \frac{1}{2\Lambda} \left[\frac{\alpha}{\Lambda} + 2\beta n \Lambda^2 + \gamma \Lambda \right] + \frac{n'(\Lambda)}{2n} \left[-\frac{2\alpha}{\Lambda} + \beta n + 3\beta n \Lambda^2 + 2\gamma \Lambda \right]
 \end{aligned} \tag{65}$$

This has the solution

$$Q_n = A \frac{\sqrt{\alpha^3 \Lambda_n} (\Lambda_n + 1)^2}{(\alpha - \gamma \Lambda_n) \sqrt{\alpha(2\Lambda_n + 1) - \gamma \Lambda_n^2}} \tag{66}$$

where we have inserted the factor $\sqrt{\alpha^3}$ so the definition of A reduces to that used in the $\gamma = 0$ case.

The last step is to match to the low- n recursion relation solution. For $\beta n \ll 1$, the WKB solution reduces to

$$P_n \approx \frac{2A \sqrt{\alpha(\alpha + \gamma)}}{\beta n} \left(\frac{\alpha}{\gamma} \right)^n \tag{67}$$

Comparing this to Eq. (60), we get

$$A = \frac{\gamma \beta}{2(\alpha - \gamma) \sqrt{\alpha(\alpha + \gamma)}} P_1 \tag{68}$$

We now need to calculate P_{tot} . Near the stable point, $n = (\alpha - \gamma)/\beta$,

$$P_n = 4 \sqrt{\frac{\alpha^3}{3\alpha - \gamma}} \frac{A}{\alpha - \gamma} e^{\Delta S} e^{-\frac{\beta}{3\alpha - \gamma} \left(n - \frac{\alpha - \gamma}{\beta} \right)^2} \tag{69}$$

which gives

$$P_{\text{tot}} = 4 \sqrt{\frac{\pi \alpha^3}{\beta}} \frac{A}{\alpha - \gamma} e^{\Delta S}$$

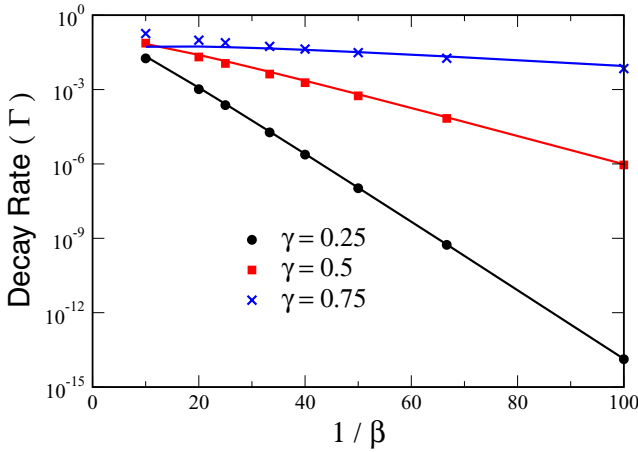


Fig. 10. (color online) The calculated decay rate Γ as a function of $1/\beta$, Eq. (71) for $\alpha = 1$, $\gamma = 0.25$, 0.5, and 0.75 (solid line) together with the exact numerical results (markers).

$$= \sqrt{\frac{\pi\beta}{\alpha + \gamma} \frac{2\alpha\gamma}{(\alpha - \gamma)^2}} P_1 e^{\Delta S} \tag{70}$$

The total probability flux out of the system is $\gamma P_1 + \beta P_2$. Since P_2 is of order 1 relative to P_1 , the β contribution to the flux is negligible, and so

$$\Gamma = \frac{\gamma P_1}{P_{\text{tot}}} = \sqrt{\frac{\alpha + \gamma}{\pi\beta} \frac{(\alpha - \gamma)^2}{2\alpha}} e^{-\Delta S} \tag{71}$$

This result is tested against the exact numerical answer in Fig. 10. The results are again quite good, with the quality decreasing as γ approaches α (for fixed β) as expected due to the decreasing equilibrium number of particles. The astute reader will note that our expression for Γ reduces in the $\gamma \rightarrow 0$ limit to our $\gamma = 0$ result above, even though some intermediate expressions (for example, the probability flux) do not correspond. We also note that the maximum value of Λ is α/γ , which approaches 1 as γ approaches the threshold value of α . Thus, near threshold, the Fokker-Planck equation and the WKB treatment coincide. Of course, this solution still has to be matched to the low/intermediate- n solution to obtain the correct prefactor.

It should also be noted that Doering et al.⁽⁷⁾ investigated a class of models wherein all transitions are single-particle transitions, as opposed to the models investigated herein, which include a 2 particle annihilation process. This entire class of models can also be easily treated via our WKB method, and yields identical results to those of Doering et al. Writing the birth term in the master equation by α_n and the death term by γ_n , the WKB solution can be written down for a very

broad class of models where $\alpha_n = (1/\beta)\tilde{\alpha}(\beta n)$ and $\gamma_n = (1/\beta)\tilde{\beta}(n)$, and $\tilde{\alpha}$, $\tilde{\beta}$ are smooth functions. In this case, the system admits a macroscopic metastable state with a large number of particles for small β . In particular, we find

$$\Lambda_n = \frac{\alpha_n}{\gamma_n} \quad (72)$$

so that

$$S_n = \int_0^n \ln(\Lambda_n) dn \quad (73)$$

The Q_n factor is:

$$Q_n = \frac{A}{\sqrt{\alpha_n \gamma_n}} \quad (74)$$

which, upon matching to the low/intermediate- n result gives (up to an obvious typographical error) the result in Doering et al. The advantage of the WKB method is that it generalizes to the multi-particle transition case.

4. THRESHOLD CASE AND THE LIFETIME OF A NEUTRAL MUTATION

In this section let us consider the threshold case, $\alpha = \gamma$. This case corresponds to the dynamics of a neutral mutation and has recently become the focus of extensive research, mainly in connection with Hubbell's unified neutral theory of biodiversity and biogeography.⁽¹⁰⁾ Here, as we already saw for the near-threshold case, the P_n 's are smooth and allow for a Fokker-Planck treatment. However, in this case the decay rate Γ is not exponentially small, and so cannot be ignored. First, let us consider what happens in the absence of β . This problem was worked out by Pechenik and Levine (P-L).⁽¹⁶⁾ They find that the mean number of particles is conserved and the variance grows linearly in time. Furthermore, the system exhibits a power-law ($1/t$) convergence to the empty state, and not an exponential dependence. This is indicative of a scale invariance in the problem. The β term serves to break this scale invariance, and gives a well-defined scale for the number of particles (for those replicas which still survive). The original Fokker-Planck equation (ignoring boundary terms) was

$$\frac{\partial P}{\partial t} = \alpha \frac{\partial^2}{\partial n^2} (nP) \quad (75)$$

The β process introduces two new terms into the FP equation, arising from the Taylor expansion of $\frac{1}{2}\beta(-n(n-1)P(n) + (n+2)(n+1)P(n+2))$ in the master equation. The first of these terms is a drift term, $\beta \frac{\partial}{\partial n} (n^2 P)$. This is responsible for the term in the mean-field equation. The second term is a diffusion term. If we

assume β small, then the additional diffusion induced by β can be ignored, and we are left with only the drift term. The new FP equation now reads

$$\frac{\partial P}{\partial t} = -\Lambda P = \alpha \frac{\partial^2}{\partial n^2}(nP) + \beta \frac{\partial}{\partial n}(n^2 P) \quad (76)$$

We have assumed the time dependence is exponential, and are looking for the smallest eigenvalue Λ . We shall see that Λ vanishes in the $\beta \rightarrow 0$ limit, consistent with the power-law behavior found by P-L.

It is useful to transform the FP equation to Shroedinger form. The first step in this process is to change variables to $x \equiv \sqrt{n}$. This yields the equation

$$-\alpha P'' - \left(\frac{3\alpha}{x} + 2\beta x^3\right) P' - 8\beta x^2 P = 4\Gamma P \quad (77)$$

The next step is a similarity transformation to eliminate the first derivative

$$P \equiv x^{-3/2} e^{-\beta x^4/4\alpha} Q \quad (78)$$

yielding the Schroedinger equation

$$-Q'' + \left(\frac{3}{4x^2} - \frac{2\beta x^2}{\alpha} + \frac{\beta^2 x^6}{\alpha^2}\right) Q = \frac{4\Gamma}{\alpha} Q \quad (79)$$

Clearly, in the absence of β there is no bound state. Rather there is a continuum that starts at zero. The potential with β has a single minimum, which is negative. Nevertheless, the ground state energy is positive, yielding a decay rate. The scaling of the decay rate is clear; by rescaling $y \equiv (\beta/\alpha)^{1/4} x$, β and α disappear from the equation, with the decay rate scaling as $\sqrt{\alpha\beta}$. As advertised, we verify the vanishing of Λ with β . The presence of β has set the scale of (the surviving) n 's, namely $\sqrt{\alpha/\beta}$, which is large for small β . Lastly, the $1/x^2$ nature of the α potential is clearly a result of the scale-free nature of the $\beta = 0$ problem. To get the prefactor multiplying the $\sqrt{\beta}$, we have to numerically solve the rescaled Shroedinger equation, (i.e., Eq. (79) with $\alpha = \beta = 1$) yielding the result

$$\Gamma = 1.111\sqrt{\alpha\beta} \quad (80)$$

The resulting scaled P_n is shown in Fig. 11, together with the rescaled exact numerical solution of the master equation for $\beta = 0.01$. We see that P_n is strongly peaked at the origin, corresponding to the zero particle mean-field solution.

The scaling with β we obtained is the same as found by Doering et al. However, as opposed to the other cases examined herein, the prefactor is different as now the mean time to extinction is not simply the inverse of the decay rate. This is due to the fact that all the eigenvalues of the master equation scale as $\sqrt{\beta}$, whereas the other cases exhibited a single exponentially small eigenvalue.

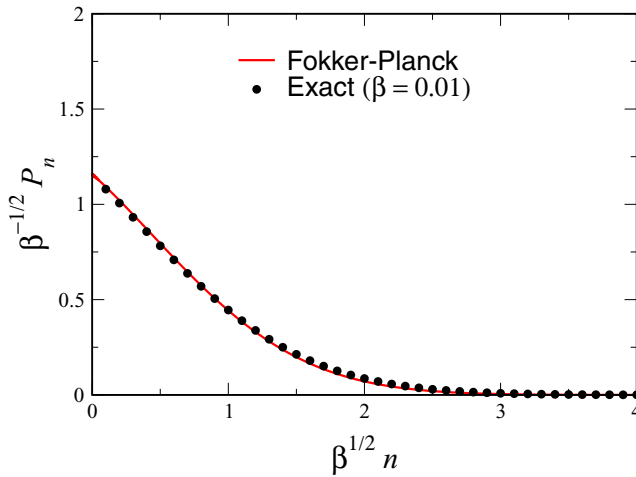


Fig. 11. (color online) Rescaled probability distribution $\beta^{-1/2} P_n$ as a function of $\beta^{1/2} n$ for the case $\alpha = \gamma = 1$, $\beta = 0.01$, together with the numerical solution of the Fokker-Planck equation.

5. CONCLUSIONS

We have solved for the fluctuation-induced extinction rates of various models exhibiting a macroscopic metastable state. Our primary methodology is use the WKB method for difference equations to directly solve the master equation. This WKB solution then has to be matched to the low- n P_n 's, since the WKB method is a large n approximation. This technique is quite general and straightforward to implement, and produces quite accurate results as long as there are not too few particles in the metastable state. It reproduces the Doering et al. results for the case of general one-particle transitions and generalizes to higher-order transitions. We have also shown the unique mathematical properties of the even/odd parity conserving model, where we are able to generate the full asymptotic expansion for the decay rate to all orders, and even to resum this divergent asymptotic series.

Our procedure as we have presented it is only directly applicable to single species problems. For the case when more than one species is fluctuating, the leading order WKB eikonal equation can be obtained.^(6,8) This equation, of Hamilton-Jacobi form, can be solved using the method of characteristics. The characteristics are given by the solutions to the classical Hamiltonian dynamics of an auxiliary problem in a $2N_s$ dimensional phase space, where N_s is the number of species.^(6,8) The leading-order exponential decay rate is then the classical action of an instanton-type solution in this space. The extension of this procedure to obtain the full physical optics solution is under current investigation.

One interesting point which arises from our analysis is the sensitivity of the decay rate to the exact form of the microscopic dynamics. This is apparent in the very different dominant $e^{\Delta S}$ for the case of the parity and non-parity cases. This is also the case when one compares the logistic model with spontaneous decay studied in Sec. 3, to the same model where the collision process $P + P \rightarrow 0$ is replaced by $P + P \rightarrow P$ at twice the rate. Even at the level of the Fokker-Planck dynamics valid near the metastable state, the widths of the distributions are different, with the variance $(3\alpha - \gamma)/2\beta$ being replaced by α/β . The values of ΔS in the two cases are very different, where Eq. (63) for the two-particle annihilation should be compared to

$$\Delta S = \int_0^{(\alpha-\gamma)/\beta} \ln\left(\frac{\alpha}{\gamma + \beta n}\right) = \frac{\alpha - \gamma}{\beta} - \frac{\gamma}{\beta} \ln\left(\frac{\alpha}{\gamma}\right) \tag{81}$$

Thus, while the two expressions agree near threshold, where the Fokker-Planck description is sufficient, as γ approaches 0, $\Delta S \rightarrow 2\alpha/\beta(1 - \ln(2))$ for the two-particle annihilation case, as we saw in Sec. 1, whereas $\Delta S \rightarrow \alpha/\beta$, almost twice as large, for small γ in the $P + P \rightarrow P$ case. Parenthetically, it should be noted that the small γ limit is very singular in this latter case, as naively Γ seems to diverge as $\gamma^{-1/2}$ for small $\gamma \ll \beta$. In general, for small β and γ , the decay rate can be shown to be given by

$$\Gamma \approx \left(\frac{\alpha}{\beta}\right)^{\gamma/\beta} \frac{a}{\Gamma(\gamma/\beta)} e^{-\alpha/\beta} \tag{82}$$

as so indeed vanishes as $\gamma \rightarrow 0$, since there is no extinction in this case. In situations where the Fokker-Planck equation is valid all the way down to $n = 0$, as we saw was the case at threshold, at least the problem is parameterized by only two parameters, the center and width of the Gaussian. However, in general, the entire function $n(\Lambda)$ is involved in the calculation of ΔS . This should have important implications for the study of extinctions in the ecological community, for example, where reliable microscopic models are difficult if not impossible to obtain.

ACKNOWLEDGMENTS

The authors thank B. Meerson and M. Assaf for sharing their work prior to publication. The work of DAK is supported in part by the Israel Science Foundation. The work of NMS is supported in part by the EU 6th framework CO3 pathfinder.

REFERENCES

1. C. W. Gardiner, *Handbook of Stochastic Methods* (Springer, Berlin 1985).
2. G. V. Grimm and C. Wissel, *Oikos* **105**:501 (2004).

3. P. Foley, Extinction models for local population. In: I. A. Hanski and M. E. Gilpin (eds.), *Metapopulation Biology - Ecology, Genetics and Evolution*, (Academic Press, London, 1997).
4. See, e.g., B. Drossel, *Adv. Phys.* **50**:209 (2001) and references therein.
5. See, e.g., M. J. Keeling and B. T. Grenfell, *Science* **275**:65 (1997); M. Lipsitch *et al.* *Science* **300**:1966 (2003); J. O. Lloyd-Smith, S. J. Schreiber, P. E. Kopp, and W. M. Getz, *Nature* **438**:355 (2005).
6. V. Elgart and A. Kamenev, *Phys. Rev. E* **70**:41106 (2004).
7. C. R. Doering, K. V. Sargsyan, and L. M. Sander, *Multi-scale Model. Simul.* **3**:283 (2005).
8. M. I. Dykman, E. Mori, J. Ross, and P. M. Hunt, *J. Chem. Phys.* **100**:5735 (1994).
9. M. Assaf and B. Meerson, *Phys. Rev. E* **74**:041115 (2006); *Phys. Rev. Lett.* **97**:200602 (2006).
10. S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton University Press, Princeton, NJ, 2001).
11. M. Doi, *J. Phys. A* **9**:1465 (1976); L. Peliti, *J. Physique* **36**:1469 (1985).
12. J. L. Cardy and U. C. Tauber, *Phys. Rev. Lett.* **77**:4780 (1996); J. L. Cardy and U. C. Tauber, *J. Stat. Phys.* **90**:1 (1998).
13. N. G. van Kampen, *Stochastic Processes in Physics and Chemistry* (North-Holland, Amsterdam, 1992).
14. C. M. Bender and S. A. Orszag, *Advanced Mathematical Methods for Scientists and Engineers* (Springer, New York, 2005).
15. For details, see <http://www.caam.rice.edu/software/ARPACK>.
16. L. Pechevnik and H. Levine, *Phys. Rev. E* **59**:3893 (1999).