

## STATIONARY DISTRIBUTION OF POPULATION SIZE IN *TRIBOLIUM*

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We propose the use of a stationary probability distribution for the analysis of data on population size. Predicting this long term population property from short term individual events is accomplished by the use of the asymptotic theory of stochastic processes. A WKB approximation to the stationary density is obtained and then applied to observations on the flour beetle *Tribolium*.

**1. Introduction.** Twenty-seven years ago, Leslie (1962) recognized that his *idea* for the analysis of the observed single species population growth data in the flour beetle *Tribolium* was far more important than the specific model that he had constructed. Leslie proposed that the equilibrium number of adult beetles should be characterized in terms of a steady-state probability distribution. While his particular model was unable to reproduce the form of the four observed distributions given to him by Park (1954), Leslie was unwilling to cast aside the utility of a steady state population distribution. In Leslie's two final scientific publications (Park *et al.*, 1964; Leslie *et al.*, 1968), 10 additional observed distributions were presented but, perhaps somewhat disappointed by his 1962 work, no further attempt was made to mathematically describe this information. It is in the tradition set by Leslie (1962) that we pursue the concept of an equilibrium probability distribution for the analysis of population density. In particular, we provide a new method for computing the steady state distribution that compliments existing procedures (Dennis and Costantino, 1988) and is directly related to the biology of the organism.

Our purpose in this paper is the development of a method for predicting long

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term population properties from short term individual events. We accomplish this by the use of methods from the asymptotic theory of stochastic processes, taking advantage of the disparate scales between the population (many individuals) and single individuals. In doing so, we hope to both illustrate the utility of such asymptotic methods when dealing with stochastic processes and make such methods more accessible to the biological community.

We begin with the experimental observations. In the third section, we provide the motivation for our use of a stochastic model and summarize previous approaches to the analysis of the data. Our stochastic theory begins in the fourth section, where we formulate the equation that characterizes the evolution of population density in terms of individual events. We solve this equation by the use of asymptotic methods in the fifth section and then compare our results with the experimental observations. We conclude with a discussion of the results.

**2. Experimental Observations.** Cultures of the flour beetle *Tribolium* can be maintained in the laboratory for long periods of time. Often the cultures are censused at regular intervals and the resulting time series record of the number of eggs, larvae, pupae and adults are the data studied. As an example, we present the observations collected by Lloyd (1965; 1968).

Twelve individual replicates of the Chicago strain of *Tribolium castaneum* (Herbst) were initiated with 13 very small larvae (4–5 days old), 10 small larvae (13–14 days old), 8 medium larvae (22–23 days old), 7 large larvae (about 32 days old), 4 sexually immature adults (0–1 day after eclosion, sexes equal) and 4 mature adults (9–10 days after eclosion, sexes equal). The cultures were maintained for 36 weeks in incubators at  $24 \pm 0.6^\circ\text{C}$  and  $31 \pm 5\%$  relative humidity. At weekly intervals the cultures were removed from the incubator and censused. All of the life stages were counted and then all living stages were returned to fresh medium.

A census record for one replicate, sketched in Fig. 1, is representative of the 12 observed population histories: The numbers of immature life stages show clear oscillations during the entire experiment while the number of adults initially increased and then appear to be much more uniform in number than the small-medium larvae and large larvae-pupae.

In the past, two approaches have been employed to study this type of data. One view considered all of the various life stages and attempted to reproduce the observed temporal pattern of egg, larval, pupal and adult numbers (Stanley, 1932; Landahl, 1955; Taylor, 1971; Fujii, 1978). Some success was realized but a nagging uneasiness remained for the models were complex and general analytical results could not be obtained. Recently, Hastings and Costantino (1987) and Desharnais and Liu (1987), were able to construct somewhat more analytically tractable age-structured models. We have

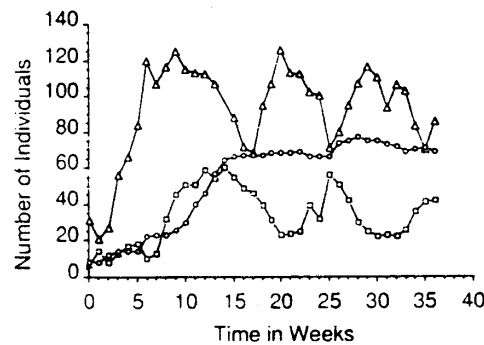


Figure 1. Population census record for one replicate of the Chicago strain of *T. cataneum*. Circles indicate the number of adults, triangles the number of small plus medium larvae and squares the number of large larvae plus pupae. (From Lloyd 1965, replicate A4.)

proposed (Hastings and Costantino, 1987), for example, that the observed demographic patterns in laboratory populations of *Tribolium* may be due to the existence of a Hopf bifurcation so that cultures can exhibit dynamic behaviors ranging from fixed point equilibria to stable limit cycles.

The second approach to the analysis of the data in Fig. 1, and the one we pursue in this report, focused exclusively on the adult life stage (Neyman *et al.*, 1956; Bartlett, 1957; 1960; Leslie, 1962; Park *et al.*, 1964; Leslie *et al.*, 1968; Lloyd, 1968; Desharnais and Costantino, 1982; 1985; Dennis and Costantino, 1988). In this case the models attempt to explain the changes in the size of the adult beetle population based on the association between the number of adults and the number of the progeny produced by these adults.

**3. Previous Analytical Work: Adult Stage Models.** We now briefly review previous work based on "adult only" models. We begin by writing an ordinary differential equation for the rate of change in adult numbers.

Let  $A^*(t)$  denote the number of adult beetles at time  $t$  and  $C$  denote the probability that a single adult prevents a potential recruit from entering the adult population (for example, by cannibalism) in some small time interval  $(t, t + dt)$ . Assuming that the adults act independently, the proportion of potential recruits that become adults during this time interval will be  $(1 - C)^{A^*(t)}$  which for small values of  $C$  is approximately equal to  $e^{-CA^*(t)}$ . If we define  $B$  as the rate at which potential recruits are produced per adult and  $D$  as the adult mortality rate then the change in adult numbers during  $(t, t + dt)$ , which equals  $A^*(t + dt) - A^*(t)$  and is denoted  $dA^*(t)$ , is given by:

$$dA^*(t) = A^*(t) [Be^{-CA^*(t)} - D] dt + o(dt), \quad (1)$$

here  $o(dt)$  represents terms such that  $o(dt)/dt \rightarrow 0$  as  $dt \rightarrow 0$ . Dividing by  $dt$  and letting  $dt \rightarrow 0$  gives the following deterministic differential equation as a model for the dynamics of the number of adult flour beetles:

$$dA^*(t)/dt = A^*(t) [Be^{-CA^*(t)} - D]. \quad (2)$$

The qualitative behavior of the differential equation (2) is straightforward. There exist two equilibria:

$$A_0^* = 0. \quad (3)$$

$$A_1^* = [\log(B/D)]/C. \quad (4)$$

If  $A^*(t)$  is non-negative and  $B > D$  then the first steady-state population is unstable while the second is stable. If  $D \geq B$  then  $A_0^* = 0$  is the only non-negative stable steady-state population equilibrium.

If the population actually followed (2), then all steady state distributions would be concentrated at a single point. The data do not exhibit this property; instead they fluctuate about an average value (see Fig. 1).

We construct the observed "stationary distribution of the population" in the following way: in our illustrative example, the data are the number of adults observed in each of the 12 independent replicate cultures during the 17 week "steady-state" interval from week 20 to the end of the experiment at week 36. Arranged in seven class intervals, the adult numbers recorded for all of the replicates were used to establish the grouped frequency counts  $x_1, x_2, \dots, x_7$  where the total number of observations  $n = \sum x_i = 204$ . These  $x_i$  values constitute the observed grouped frequency distribution for this data set (see the histogram in Fig. 2).

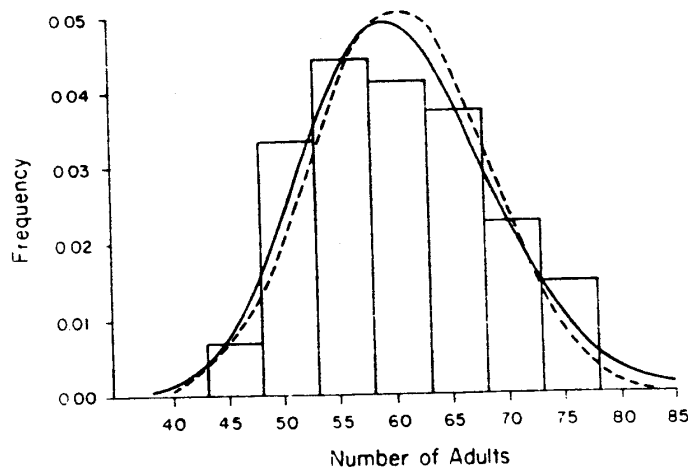


Figure 2. Observed grouped frequency distribution (histogram). The fitted gamma probability density function (smooth curve) and the WKB approximate stationary density (dashed curve).

These data (see Costantino and Desharnais, 1981; Desharnais and Costantino, 1982; 1985; Dennis and Costantino, 1988 for an extensive presentation of additional data sets) provide the motivation for our use of a stochastic analysis. Our objective in studying the stochastic dynamics of adult

numbers is to make use of the observed variability as an additional source of information about the population.

One way of theoretically constructing such stationary distributions is to convert (2) to a stochastic differential equation (Costantino and Desharnais, 1981; Desharnais and Costantino, 1985; Dennis and Patil, 1984; Dennis and Costantino, 1988). We write:

$$dA^* = A^*[Be^{-Ca^*} - D] dt + \sigma(A^*)^{1/2} dW. \quad (5)$$

Here  $dW = W(t+dt) - W(t)$  is the increment of the Wiener or Brownian motion process:  $dW$  is normally distributed with mean 0 and variance  $dt$ . The term  $\sigma(A^*)$  is a function of population size. For example, a commonly chosen form is  $\sigma_0 A^{1/2}$  where  $\sigma_0$  is a constant.

If the model (5) is accepted, then we introduce the density  $v(a, t)$  defined by:

$$v(a, t) da = Pr[a \leq A^*(t) \leq a + da], \quad (6)$$

and which satisfies (Gardiner, 1983):

$$\partial v / \partial t = -\partial[a(Be^{-Ca} - D)v] / \partial a + \frac{1}{2} \partial^2[\sigma(a)v] / \partial a^2. \quad (7)$$

Since (7) is a diffusion equation, we will call (5) a "diffusion approximation".

The stationary distribution for a stochastic differential equation model with fluctuations that scale with  $A^*$  can be approximated using the gamma probability density (Costantino and Desharnais, 1981; Dennis and Costantino, 1988). In that work, the gamma density is fit to the observed data using two parameters that characterize shape and scale [or mean and coefficient of variation—see Mangel (1985) for a discussion of the gamma density as a general ecological model]. Although these estimated parameters are functions of the underlying biological parameters, there are two known quantities and more than two unknowns, which means that we cannot estimate all of the biological parameters from the stationary gamma model. Thus, there is a need to proceed in the other direction: to begin with the biological model and construct the stationary density from first principles.

That is, another way of establishing stationary distributions is by using a stochastic birth-death process to formulate flour beetle growth (Desharnais and Costantino, 1982). That is the approach taken in this paper. The methods we introduce will allow us to study the validity of the diffusion approximation and connect the fluctuation function  $\sigma(A)$  to the underlying population processes. Our work is similar to that of Roozen (1987), who begins with a birth-and-death process model for population dynamics and expands the resulting master equation to obtain a Fokker-Planck equation which is solved by asymptotic methods. We will, however, solve the master equation directly.

We see the stochastic differential equation and birth-death formulations as

complimentary and mutually reinforcing. Certainly from an experimental point of view, it is very important to provide strong theoretical support for the application of the concept of a stationary distribution in population research.

4. *Formulation of the Master Equation.* We assume that the number of adults  $A^*(t)$  in the population is a Markov process. Our methods are easily extended to include all life stages, if that is what is needed to insure a Markov model. Details are found in Peters (1987). We introduce a transition function:

$$\begin{aligned} \Pr[A^*(t+dt)=a+j|A^*(t)=a], \\ = p_j(a) dt + o(dt), \end{aligned} \quad (8)$$

here  $j$  takes integer values. We will concentrate on single step processes for which  $j = -1, 0, 1$  and denote:

$$\begin{aligned} r^*(a) &= \Pr[A^*(t+dt)=a+1|A^*(t)=a]/dt \\ l^*(a) &= \Pr[A^*(t+dt)=a-1|A^*(t)=a]/dt \end{aligned} \quad (9)$$

We define the equilibrium population  $\Phi$  by:

$$r^*(\Phi) = l^*(\Phi) \quad (10)$$

and scale  $A^*(t)$  by  $\Phi$ . Thus we introduce:

$$A(t) = A^*(t)/\Phi. \quad (11)$$

The spacing between jumps in the scaled density  $A(t)$  is now:

$$\varepsilon = 1/\Phi. \quad (12)$$

Notice that  $\varepsilon$  becomes small as  $\Phi$  becomes large. We assume that the size of a jump is small compared to the size of the system, which is represented here by the equilibrium density  $\Phi$ . Let us now define  $l(a)$  and  $r(a)$  by:

$$l(a) = l^*(\Phi a), \quad (13)$$

and:

$$r(a) = r^*(\Phi a). \quad (14)$$

The stochastic dynamics of  $A(t)$  can be written compactly as:

$$A(t+dt) = \begin{cases} A(t) + \varepsilon & \text{with probability } r(A(t)) dt + o(dt) \\ A(t) - \varepsilon & \text{with probability } l(A(t)) dt + o(dt) \\ A(t) & \text{with probability } 1 - [r(A(t)) + l(A(t))] dt + o(dt). \end{cases} \quad (15)$$

As before let  $v(a, t) da$  be the probability that  $a \leq A(t) \leq a + da$ . Then  $v(a, t)$

satisfies the following "master equation" obtained by balancing probabilities (Gardiner, 1983; van Kampen, 1981):

$$v(a, t + dt) = v(a - \varepsilon, t)r(a - \varepsilon) dt + v(a + \varepsilon, t)l(a + \varepsilon) dt + v(a, t)[1 - [r(a) + l(a)] dt] + o(dt). \quad (16)$$

In words, equation (16) states that the probability of having  $a$  adults at time  $t + dt$  is equal to the probability of having  $a - \varepsilon$  adults at time  $t$  and experiencing an increment  $\varepsilon$  in the next  $dt$  plus the probability of having  $a + \varepsilon$  adults in the previous time period and experiencing a decrement of  $\varepsilon$  plus the probability of having precisely  $a$  adults at time  $t$  and experiencing neither a birth or death in the next  $dt$ .

To derive a differential-difference equation, we subtract  $v(a, t)$  from both sides of (16) and divide by  $dt$  to obtain:

$$[v(a, t + dt) - v(a, t)]/dt = v(a - \varepsilon, t)r(a - \varepsilon) + v(a + \varepsilon, t)l(a + \varepsilon) - v(a, t)[r(a) + l(a)] + o(dt)/dt. \quad (17)$$

Letting  $dt \rightarrow 0$  gives the differential-difference equation:

$$v_t = v(a - \varepsilon, t)r(a - \varepsilon) + v(a + \varepsilon, t)l(a + \varepsilon) - v(a, t)[r(a) + l(a)]. \quad (18)$$

The stationary solution of this equation satisfies  $v_t = 0$ . We then rewrite (18) as:

$$0 = v(a - \varepsilon)r(a - \varepsilon) + v(a + \varepsilon)l(a + \varepsilon) - v(a)[r(a) + l(a)]. \quad (19)$$

We call (18) or (19) master equations. They are similar to the Chapman-Kolmogorov equations (Gardner, 1983; van Kampen, 1981). Our problem is to solve (19) for the stationary density function.

**5. WKB Approximation to the Stationary Density.** We will now construct an approximate solution of (19) by exploiting the smallness of  $\varepsilon$ . We do this by use of the WKB method (Bender and Orszag, 1983).

A WKB approximation is of the form:

$$v(a) \approx k(a)e^{-[\Theta(a)/\varepsilon]}, \quad (20)$$

where  $k(a) = \sum k_i(a)\varepsilon^i$  and  $\Theta(a)$  are functions to be determined. It is called WKB after the theoretical physicists Wenzel, Kramers and Brillouin who, during the 1920s, popularized its use in solving quantum mechanical differential equations with a small parameter. Generalizations of this ansatz have been used since then to obtain asymptotic approximations to linear partial differential equations (see Keller, 1978; Cohen and Lewis, 1967), as well as difference equations such as equation (18) (Knessl *et al.*, 1984). The ansatz (20)

is inserted into equation (19) and the coefficients of successively higher powers of  $\varepsilon$  are set equal to zero.

Let  $v_k(a)$  denote the first term of our approximate solution to (19):

$$v_k(a) = [k_0(a) + O(\varepsilon)]e^{-[\Theta(a)/\varepsilon]}. \quad (21)$$

We substitute this into equation (19), collect terms according to powers of  $\varepsilon$  and set the coefficient of  $\varepsilon^0$  equal to 0 to obtain:

$$r(a)e^{\Theta_a} + l(a)e^{-\Theta_a} - [l(a) + r(a)] = 0. \quad (22)$$

This is the eikonal equation (see Cohen and Lewis, 1967; Keller, 1978) for  $\Theta(a)$ ; a partial derivative is indicated by a subscript. The coefficient of  $\varepsilon^1$  vanishes if  $k_0$  satisfies the "transport" equation:

$$[r(a)e^{\Theta_a} - l(a)e^{-\Theta_a}]k_{0a} + \left[\frac{1}{2}[r(a)e^{\Theta_a} + l(a)e^{-\Theta_a}]\Theta_{aa} + r_a(a)e^{\Theta_a} - l_a(a)e^{-\Theta_a}\right]k_0 = 0. \quad (23)$$

We solve (22) by inspection, noting that its solution is (Knessl *et al.*, 1984):

$$\Theta(a) \propto \exp\left[(-1/\varepsilon) \int_0^a \log[l(s)/r(s)] ds\right].$$

Using this we solve (23) which is a linear, first order equation for  $k_0(a)$ . Following this procedure, we find that the leading order term of the WKB approximation to the difference equation (19) is:

$$v_k(a) = n[l(a)r(a)]^{-1/2} \exp\left[(-1/\varepsilon) \int_0^a \log[l(s)/r(s)] ds\right], \quad (24)$$

where  $n$  is a constant chosen so that  $v_k(a)$  is a probability density for population size. The higher order terms of this asymptotic approximation can be computed to any desired degree of precision by using the WKB ansatz:

$$v(a) = \sum_{i=0}^{\infty} k_i(a)\varepsilon^i e^{-[\Theta(a)/\varepsilon]}. \quad (25)$$

In order to use this approximation to the stationary density in (24), the functions  $r$  and  $l$  must be specified. Equation (1) suggests that for the flour beetle *Tribolium* we choose:

$$\begin{aligned} r(a) &= B(\Phi a)e^{-C(\Phi a)}, \\ l(a) &= D(\Phi a). \end{aligned} \quad (26)$$



Desharnais and Costantino (1982) noted that if such birth and death rates were used the origin becomes an absorbing state. In the steady state this means the population will go extinct with certainty. To avoid extinction they used:

$$\begin{aligned}r(a) &= B(\Phi a + 1)e^{-C(\Phi a)}, \\l(a) &= D(\Phi a),\end{aligned}\tag{27}$$

thus slightly increasing the birth rate. Their justification is that single species laboratory cultures of beetles rarely go extinct. Of course, laboratory experiments are of finite duration, but they calculated the mean time to extinction for a birth-death process with the  $r$  and  $l$  as in (27) to be on the order of  $10^{21}$  years so that in practical terms there is a steady-state distribution.

Here we modify (27) by letting:

$$\begin{aligned}r(a) &= B(\Phi a + \delta)e^{-C(\Phi a)}, \\l(a) &= D(\Phi a),\end{aligned}\tag{28}$$

where the new parameter  $\delta$ , which implicitly accounts for the multistage life history of *Tribolium*, is determined in the following way. Note that  $r(0) = B\delta$ , so that even when there are no adults present there is still a chance of the appearance of new adults. In this case  $\delta$  is a measure of the rate of adult emergence from the pre-adult stages (eggs, pupae, larvae). Hence even if the adults disappear, temporarily, there are potential adults waiting to mature. We can relate the mean time,  $T$ , for an egg to mature into an adult to the adult emergence rate  $\delta$  by noting that:

$$Pr[\text{one adult appears at time } t+1 | A(t)=0] = r(0) = B\delta;$$

$$Pr[\text{first adult appears at time } t+j | A(t)=0] = (1 - B\delta)^j B\delta.$$

Hence:

$$T = E[\text{time for adult to appear} | A(t)=0] = \sum_{j=1}^{\infty} (1 - B\delta)^j B\delta j. \tag{29}$$

From equation (29), we find that:

$$\delta \approx 1/BT. \tag{30}$$

Expression (30) is an approximation due to the assumption of independence for an adult to appear in consecutive time periods which led to the geometric distribution in (29). The parameter  $T$  is known experimentally so that we have both an interpretation and a procedure to estimate  $\delta$ .

Performing the integration in (24) and using the  $r$  and  $l$  in (28),  $v_k(a)$  is found to be:

$$v_k(a) = n_1 [l(a)r(a)]^{-1/2} [(B/D)[1 + (\delta/\Phi a)]]^{\Phi a} [a + (\delta/\Phi)]^\delta e^{-C\Phi^2 a^2/2}, \quad (31)$$

where  $n_1$  is a normalization constant chosen so that  $v_k(a)$  is a probability density.

There is a spike at the origin since  $l(0) = 0$  and therefore

$$v_k(0) = k_2 [l(0)r(0)]^{-1/2} = \infty. \quad (32)$$

Note that  $v_k(a)$  can be viewed as a probability density as long as it is integrable. For  $a$  in the interval around zero we have:

$$v_k(a) < Ka^{-1/2};$$

hence  $v_k(a)$  is integrable. However, there is no spike in the observed beetle density since populations do not often go extinct in the laboratory. To deal with this we define a conditional density:

$$\begin{aligned} v_k^\varepsilon(a) &= \text{Pr}[A(\infty) \approx a | A(\infty) > \varepsilon], \\ &= v_k(a) / \int_\varepsilon^\infty v_k(s) \, ds. \end{aligned} \quad (33)$$

The motivation is that  $A(t)$  cannot be less than  $\varepsilon$  without being zero. Hence the range of  $v_k^\varepsilon(a)$  is  $(\varepsilon, \infty)$ . As  $\varepsilon$  tends toward zero,  $v_k^\varepsilon(a)$  tends toward  $v_k^0(a)$  which is a true probability density.

**6. *T. castaneum*: Chicago Data.** Our emphasis in this note is to broaden the theoretical support for the application of stationary distributions in population biology. On the other hand, statistical inferences for the gamma abundance model, which is obtained from a stochastic differential equation argument, can be made from observed steady-state distributions (Dennis and Costantino, 1988). The statistically fitted gamma for the Chicago strain of *T. castaneum* is sketched in Fig. 2. The WKB approximation to the stationary density with parameter values  $B=0.237$ ,  $D=0.088$ ,  $C=0.0165$  and  $\delta=1$  is plotted on the same figure. The latter distribution describes the data fairly well. Other plots showing the dependence of  $v_k(a)$  on the parameters  $B$ ,  $D$  and  $C$  are given in Peters (1987). Most of the effects of the parameter changes can be predicted *a priori*; but one interesting effect is that as  $C$  increases the variance of  $v_k(a)$  decreases. In other words, as the magnitude of the density regulation is increased the observed fluctuations in population size are expected to be reduced. It is heartening to report that the parameter dependencies of the stationary solution  $v_k(a)$  are in agreement with those based on the two different

gamma approximations to the stationary distribution obtained by Costantino and Desharnais (1981) and Dennis and Costantino (1988).

**7. Discussion.** The methodology introduced here allows us to connect short time changes in individual adult numbers [measured by  $r(a)$  and  $l(a)$ ], with the ultimate, steady-state distribution of the population. It is clear that stochastic formulations—for these problems—are far superior to deterministic schemes since the latter predict point equilibria which are not observed experimentally. We believe that the birth–death formulation coupled with asymptotics provides a number of additional advantages, when compared to approaches based on stochastic differential equations. First, one avoids all of the complications of stochastic calculus, measure theory and the Ito–Stratonovich controversy. The master equation is derived directly from the underlying stochastic assumptions. For example, it is clear if we use the general transition distribution (8), the stationary density satisfies (after scaling, etc.):

$$v(a) = \sum_j v(a - \varepsilon j) p_j(a - \varepsilon j) + v(a) \left[ 1 - \sum_j p_j(a) v(a) \right]. \quad (34)$$

No additional conceptual machinery is needed. Second, the birth–death formulation provides a natural connection to the laboratory measurements, since the transition rates ( $p_j(a)$  or—in the simpler case— $l(a)$  and  $r(a)$ ) are associated with short time changes in the population. From these we are able to construct long term population distributions not just point equilibria. Third, although the asymptotic methods produce only an approximate solution of the problem, the methods are easy to use and the resulting eikonal and transport equations are easy to solve.

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## APPENDIX

*The Origin and Nature of the Diffusion Approximation to the Steady-State Distribution.* Roozen (1987) describes one way of expanding master equation (18) or (19) to obtain a diffusion approximation. Here we describe a simpler, but less rigorous, method. To begin, we Taylor expand equation (19) in powers of  $\varepsilon$ . This leads to the infinite order differential equation:

$$\sum_{n=1}^{\infty} \left[ \frac{(-\varepsilon)^n}{n!} \frac{d^n [r(a)v(a)]}{da^n} + \frac{\varepsilon^n}{n!} \frac{d^n [l(a)v(a)]}{da^n} \right] = 0. \quad (A1)$$

Since  $\varepsilon$  is small, we assume *ad hoc* that  $[\varepsilon^n d^n v] \rightarrow 0$  as  $\varepsilon \rightarrow 0$  for  $n > 3$ . We then truncate equation (A1) after 2 terms only. This gives:

$$\frac{\varepsilon}{2} \frac{d^2[v(a)(r(a)+l(a))]}{da^2} - \frac{d[v(a)(r(a)-l(a))]}{da} = 0. \quad (\text{A2})$$

Equation (A2) is the equation satisfied by a probability density that arises from the stochastic differential equation (SDE):

$$dA = [r(A) - l(A)] dt + [\varepsilon[r(A) + l(A)]]^{1/2} dW. \quad (\text{A3})$$

Comparing equations (A3) and (5) shows that we can set:

$$r(A) - l(A) = A[Be^{-cA} - D]$$

and:

$$\sigma(A) = r(A) + l(A).$$

We thus have a way to connect the fluctuations,  $\sigma(A)$ , and the mean dynamics,  $A[Be^{-cA} - D]$ , in the SDEs (A3) and (5) through the fundamental birth and death process.

We let  $v_d(a)$  denote the solution of equation (A2), and find it by two quadratures

$$v_d(a) = k_2 \exp\left[-\int_0^a h(s) ds\right], \quad (\text{A4})$$

where:

$$h(a) = \frac{[r'(a) + l'(a)] - (2/\varepsilon)[r(a) - l(a)]}{r(a) + l(a)}. \quad (\text{A5})$$

To compare  $v_d(a)$  and  $v_k(a)$  we use a WKB approximation to the linear partial differential equation (A2) of the form:

$$v_d(a) \approx k_d(a) \exp[-\Theta_d(a)/\varepsilon]. \quad (\text{A6})$$

When this is done we find:

$$\Theta_d(a) = 2 \int_0^a [l(s) - r(s)]/[l(s) + r(s)] ds. \quad (\text{A7})$$

This expression is to be compared to its counterpart in (24), which will be denoted as  $\Theta_k(a)$ :

$$\Theta_k(a) = \int_0^a \log[l(s)/r(s)] ds. \quad (\text{A8})$$

Knessl *et al.* (1984) noted that  $\Theta_k(a) > \Theta_d(a)$  except at  $a=0$  implying that  $v_d(a)$  will be more diffuse than  $v_k(a)$ . They point out that the further away from the equilibrium population the greater the discrepancy between  $\Theta_k(a)$  and  $\Theta_d(a)$  and therefore, for small  $\varepsilon$ , the greater the difference between  $v_k(a)$  and  $v_d(a)$ . These two densities will differ most noticeably in their tails.

One reason for this discrepancy is that in the diffusion approximation we ignored moments higher than second order of  $v(a)$ . Since  $r(a)$  and  $l(a)$  depend explicitly on  $\Phi$  which is simply  $1/\varepsilon$ , truncating terms such as:

$$\varepsilon^3 \frac{d^3[r(a)v(a)]}{da^3},$$

in equation (A1) will not be justified where  $v(a)$  is changing rapidly. In the tails of the distribution  $v(a)$  changes concavity and thus the distribution will change most rapidly.

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