ALLEE EFFECTS: POPULATION GROWTH, CRITICAL DENSITY, AND THE CHANCE OF EXTINCTION

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ABSTRACT. This paper develops mathematical models to describe the growth, critical density, and extinction probability in sparse populations experiencing Allee effects. An Allee effect (or depensation) is a situation at low population densities where the per-individual growth rate is an increasing function of population density.

A potentially important mechanism causing Allee effects is a shortage of mating encounters in sparse populations. Stochastic models are proposed for predicting the probability of encounter or the frequency of encounter as a function of population density. A negative exponential function is derived as such an encounter function under very general biological assumptions, including random, regular, or aggregated spatial patterns. A rectangular hyperbola function, heretofore used in ecology as the functional response of predator feeding rate to prey density, arises from the negative exponential function when encounter probabilities are assumed heterogeneous among individuals. These encounter functions produce Allee effects when incorporated into population growth models as birth rates.

Three types of population models with encounter-limited birth rates are compared: (1) deterministic differential equations, (2) stochastic discrete birth-death processes, and (3) stochastic continuous diffusion processes. The phenomenon of a critical density, a major consequence of Allee effects, manifests itself differently in the different types of models. The critical density is a lower unstable equilibrium in the deterministic differential equation models. For the stochastic discrete birth-death processes considered here, the critical density is an inflection point in the probability of extinction plotted as a function of initial population density. In the continuous diffusion processes, the critical density becomes a local minimum (antimode) in the stationary probability distribution for population density. For both types of stochastic models, a critical density appears as an inflection point in the probability of attaining a small population density (extinction) before attaining a large one. Multiplicative ("environmental") stochastic noise amplifies Allee effects. Harvesting also amplifies those effects.

Though Allee effects are difficult to detect or measure in natural populations, their presence would seriously impact exploitation, management, and preservation of biological resources.

KEY WORDS: Allee effects, critical density, extinction, depensation, minimum viable population, endangered species, birth-death process, diffusion process.

1. Introduction. In the study of the growth, preservation, and exploitation of biological populations, it seems natural to consider the following question posed by Allee [1938, p. 107]: " ... what minimal numbers are necessary if a species is to maintain itself in nature?" The question arises when the per-individual growth rate of a species is initially an increasing function of population size, commencing at negative values for very low densities (Odum and Allee [1954]). The phenomenon, commonly termed the "Allee effect," may have a variety of causes, one being the uncertainty of mates finding each other in sparse populations (Allee [1931, 1938], Haldane [1953], Andrewartha and Birch [1954], Watt [1968]). That the union of gametes might be difficult to achieve when population members are scarce has been hypothesized for sea urchins (Allee [1931]), flour beetles (MacLagen [1932], Park [1933]), muskrats (Errington [1940]), tsetse flies (Glover et al. [1955], Glasgow [1963]), sheep ticks (Milne [1949, 1950]), whales (Hamilton [1948]), box turtles (Mosimann [1958]), condors (Mertz [1971]), acridids (Rowell [1978]), snails (Thomas and Benjamin [1974]), spruce budworms (Parker et al. [1977]), and zooplankton (Gerritsen [1980]).

Few data are available on mating rates and population growth of rare species. Laboratory population experiments occasionally have detected Allee effects due possibly to mating frequency (MacLagen [1932], Park [1933], Ullyett [1945], Snyman [1949], Watt [1960], Thomas and Benjamin [1974]). Laboratory experiments with assorted insects in mating chambers have displayed positive dependence of mating rates on population density (Nishigaki [1963], Speiss [1968], Gilliland and Davich [1968], Speiss and Speiss [1969], Otake and Oyama [1973], Eckstrand and Seiger [1975]). Positive relationships between mating rate and density have been observed for a few species in the field (Hamilton [1948], Ouye et al. [1964], Graham et al. [1965], Glover et al. [1955]). Occasionally, rare organisms proved so adept at finding each other that no effects on mating rates were detected (Teesdale

[1940], Surtees and Wright [1960], Burns [1968]).

Additionally, mathematical models relating mating rates to population growth, like rare species members, are scarce. Pioneering theoretical efforts of Volterra [1938] and Philip [1957] have been followed up only rarely (Mosimann [1958], Bradford and Philip [1970a, b], Hsu and Frederickson [1975], Pielou [1977, p. 35], Gerritsen [1980], Jacobs [1984], Lande [1987], Cushing [1988]). Parasites obligated to find mates on (or in) their hosts are the subject of some stochastic models (Andrewartha and Birch [1954, p. 338], Rohlf [1969], Plowright and Paloheimo [1977], May [1977a], Nasell [1979]).

Despite this surprising lack of empirical or mathematical attention, the possible presence of Allee effects pervades virtually all areas of population biology.

Allee effects may have inordinate influence in shaping ecological communities. Observed patterns of species packing on resource gradients contradict predictions of traditional (i.e. without Allee effects) competition theories; instead, the observed species separation could be caused by the costs of being rare (Hopf and Hopf [1985]).

In population genetics, altering theories of density-dependent natural selection to include Allee effects produces notably different predictions for gene frequency and population size changes (Asmussen [1979]).

Allee effects have likely been important selective forces in evolution. Mating shortage is a hypothesized evolutionary cause of the existence of distinct species (Bernstein et al. [1985]), sociality (Philip [1957]), sensory adaptations and habitat selection (Mosimann [1958]), "hilltopping" behavior (Shapiro [1970], Brussard and Ehrlich [1970]), and hermaphroditism and parthenogensis (Tomlinson [1966], Scudo [1969], Gerritsen [1980]).

Allee effects form crucial aspects of biological control. A common method of insect pest control is to disrupt fertilization by inundating an area with sterilized males or pheromone, thereby inducing an Allee effect in the pest population (Knipling [1955], Sower and Whitmer [1977], Beroza and Knipling [1972], Braumhover et al. [1955], Steiner et al. [1970]). Mathematical models of the sterile male technique have received attention (Costello and Taylor [1975], Prout [1978]).

The theory and practice of species preservation could be drastically

impacted by Allee effects in endangered species (Lande [1988]). Though the importance of stochastic modeling in conservation biology has been widely recognized (Shaffer [1981], Shaffer and Samson [1985], Samson et al. [1985], Wright and Hubbell [1983], Soule [1987], Goodman [1987]), the possibility that Allee effects might diminish the chance of a species' survival is seldom considered (see Lande [1987] for a rare example).

Finally, policies for harvesting living resources must be revised when faced with the prospect of Allee effects in the populations. Clark [1976, p. 16] began the book that launched "bioeconomics" with a graphical model depicting the dramatic consequences of harvesting in the presence of "depensation." Since then, theoretical policy studies of exploitation have mostly bypassed this warning and proceeded on the assumption that depensation is not an important factor (a noteworthy exception is by Reed [1978]).

In this paper I present models for addressing Allee's question on the minimal numbers necessary for a species' survival. The paper develops the concept of a species' critical density for three types of population growth models: deterministic differential equations, stochastic discrete birth-death processes, and stochastic continuous diffusion processes. The approach is to compare the dynamic behavior of deterministic and corresponding stochastic models. My emphases are on simplicity and elucidation. The numbers of parameters are kept to a minimum. I have attempted to make assumptions explicit and to provide intuitive, comparative exposition on the dynamic properties of the models. I hope this approach will facilitate field and lab investigations, enhancing the vulnerability of the models to empirical testing (Williams [1971]).

The models developed here tacitly refer to animal populations, though botanists might find portions useful in studying pollination systems. This work furthermore emphasizes dynamic models of reproduction limitation through shortage of mating encounters. Other mechanisms, though, such as physiological facilitation of reproduction in bird colonies (Schorger [1955], Chabrzyk and Coulson [1976]), protection from predation by schooling in fish (Larkin et al. [1964], Clark [1974]), enhancement of predation by attacking in groups (Berryman et al. [1985]), resistance to competition or invasion through density (such as in grasses and other plants), or loss of genetic diversity in small populations, produce similar Allee effects and are covered by these models in a phenomenological way.

The discussion is arranged as follows. §2 presents stochastic mechanisms for: (a) the probability that an organism encounters at least one other of its species, or (b) its expected frequency of encounter. Using assumptions leading to simple birth processes, functions relating the probability of encounter or frequency of encounter to population density are derived. Two particular functions are singled out for detailed analysis: the negative exponential function and the rectangular hyperbola function. §3 then incorporates the mating functions into traditional differential equation models of population growth and examines the resulting dynamic behavior. Allee's postulated lower critical density is an unstable equilibrium in such deterministic models. Harvesting of a population experiencing an Allee effect is shown to increase the critical density. §4 develops some discrete and continuous stochastic versions of the population growth models, employing the methods of birth-death processes and diffusion processes (stochastic differential equations). A critical density manifests itself in different ways when stochastic forces are incorporated in population models. In discrete birth-death processes, a critical density becomes an inflection point in the probability of extinction plotted as a function of initial population density. In continuous diffusion processes, a critical density appears as a local minimum (antimode) in the stationary probability distribution for population density.

2. Matings and population density. This section examines several mathematical expressions for the frequency of mating encounters in a population and for the probability that an organism mates one or more times. Mating frequency is modeled as a stochastic pure birth process, which allows treatment of random, aggregated, or regular spatial patterns of the population members. A negative exponential (NE) function, $1 - e^{-\beta n}$, is shown to describe quite generally the dependence of mating frequency (or mating probability) on population density, n. Random variation in the parameter β across individuals is subsequently introduced in this section. A rectangular hyperbola (RH) function, $n/(\theta + n)$, results when the random variation in β follows an exponential distribution. Both the NE and the RH encounter functions fit a published data set on copulation frequencies of azuki bean weevils. A shortage of mating encounters affects the reproductive rate of a population, so the encounter functions derived in this section are important

to the form of the birth rate term in the population growth models appearing in §3 and §4.

The BC function. Volterra ([1938], the paper is reprinted in Scudo and Ziegler [1978]) was one of the earliest to include explicit mating conditions in a population growth model. Volterra suggested that the number of meetings between the two sexes during any unit of time would be proportional to n^2, where n is the combined density of males and females. A constant sex ratio is assumed; the process is somewhat analogous to the collisions of gas molecules. The number of encounters for a given individual would be proportional to n under this scheme. This bimolecular collisions model (hereafter BC model) is included in subsequent discussions for purposes of comparison with the models proposed in this paper.

Birth process models. Stochastic fluctuations in mating encounters would affect reproduction in sparse populations. The frequency of matings for a given individual would then be best described by a discrete probability distribution rather than a deterministic function of n. Certain statistical distributions arise in this context from straightforward assumptions about the mate searching behavior of organisms.

Let a be the effective area searched by an individual female during breeding season (the area searched $\times$ proportion of males in population), and $X(a)$ the number of mating encounters a female has had (a random variable whose distribution depends on the value of a). One set of simple assumptions about the mating process is as follows: (1) the sex ratio remains constant; (2) mating is promiscuous and females mate with any males encountered; (3) the probability that a female encounters a male after searching a small area Δa is proportional to population density, n, and depends also on her previous number of encounters (in other words,

$$(2.1) \qquad Pr[X(a + \Delta a) = x + 1 | X(a) = x] = \delta(x)n\Delta a,$$

where $\delta(\cdot)$ is a non-negative function such that $\delta(0) = b$, a constant. Specific forms for δ are considered later); (4) The probability of encountering two or more males in Δa is negligible.

These assumptions specify a stochastic, homogeneous, "birth" process (see Bailey [1964, p. 84]), where the quantity being born (i.e., increasing) is the number of matings, $X(a)$. The probabilities for $X(a)$,

denoted $\Pr[X(a) = x] = p_x(a)$, satisfy the well-known system of forward equations:

$$(2.2) \qquad \frac{dp_x(a)}{da} = \delta(x-1)np_{x-1}(a) - \delta(x)np_x(a), \quad x = 0, 1, 2, \ldots,$$

with the convention that $\delta(x) = 0$ if $x < 0$. The boundary value $p_0(0) = 1$ applies since there are no matings if a is zero. Under these conditions the system (2.2) can be solved recursively for the $p_x(a)$ values, starting with $p_0(a)$ (Feller [1968, p. 476]):

$$(2.3) \qquad p_0(a) = e^{-a\delta(0)n} = e^{-abn},$$

$$(2.4) \qquad p_x(a) = e^{-a\delta(x)n}\delta(x-1)n \int_0^a e^{\delta(x)ns}p_{x-1}(s)ds.$$

Such birth processes can represent considerably more situations in nature than would appear from the seeming restrictiveness of the assumptions. For instance, if a female mates with only a certain fraction of males encountered, then the effective search area, a, or population density, n, could be modified with an appropriate scale factor. Or, if females do not search per se but remain stationary, then a could represent the diffusion area of a pheremone. In still other situations with stationary females awaiting the arrival of searching males, a may be redefined as a measure of time.

Specific forms for $\delta(x)$ will now be considered. It is reasonable to assume that $\delta(x)$ is adequately approximated for low x values by a linear function, that is, by the first terms of a Taylor series expansion around zero:

$$(2.5) \qquad \delta(x) = \delta(0) + x\delta'(0) + \cdots \approx b + cx,$$

where $c = \delta'(0)$. Three possible signs for c produce three cases.

Case 1. $c = 0$. Effectively, the earlier assumption 3 becomes: (3) The probability that a female encounters a male after searching a small area Δa is independent of her previous number of encounters, but is proportional to population density. This revised assumption is a quantitative definition of a random spatial dispersion pattern. The assumptions characterize the Poisson process, that is, equations (2.3) and (2.4) yield a Poisson distribution for $X(a)$ with parameter abn:

$$(2.6) \qquad \Pr[X(a) = x] = e^{-abn}(abn)^x/x!, \quad x = 0, 1, 2, \ldots.$$

The expected number of mating encounters for a female under the Poisson process is proportional to n :

$$(2.7) \qquad E[X(a)] = abn.$$

Thus, the deterministic BC model is retrieved as the mean of this stochastic model. Clearly both models could apply only at lower population densities. The mating ability of an organism would likely reach an upper limit (and perhaps even decline from interference) as n becomes larger.

Case 2. $c > 0$. A positive value of c represents a first-order aggregation model, with the assumption 3 revised to read: (3) The probability that a female encounters a male after searching a small area Δa increases linearly with her number of previous encounters in addition to being proportional to n. A negative binomial distribution of matings is the result:·

$$(2.8) \qquad p_x(a) = \binom{(b/c) + x - 1}{x}(e^{-acn})^{b/c}(1 - e^{-acn})^x,$$
$$x = 0, 1, 2, \cdots .$$

The expected frequency of encounters for the female increases exponentially with population density under this distribution:

$$(2.9) \qquad E[X(a)] = (b/c)(e^{acn} - 1).$$

Like Case 1, this model would also only be appropriate at low population densities.

Case 3. $c < 0$. A more uniform, or regular, spatial distribution may be represented by revising assumption 3 such that the likelihood of mating with another male in Δa declines linearly with each male encountered. This case might also represent satiation of mating activity in a female searching about a population of randomly dispersed males. The corresponding probability distribution is binomial:

(2.10)

$$p_x(a) = \binom{-b/c}{x}(1 - e^{acn})^x(e^{acn})^{-(b/c)-x}, \quad x = 0, 1, \cdots, -b/c.$$

This formula is strictly correct only if b/c is an integer; otherwise the probabilities take a type of generalized binomial form. Also, an assumption is that $\delta(x) = 0$ for values of x greater than $-b/c$.

The expected number of encounters under (2.10) reaches an upper maximum, $-b/c$, as the population density increases:

$$(2.11) \qquad\qquad E[X(a)] = (-b/c)(1 - e^{acn}).$$

This upper maximum is a realistic feature if the model is to characterize mating frequencies at high as well as low densities.

The NE function. The probability that a female does not find a mate is of interest when one mating is sufficient for her to realize full reproductive potential. This probability is given by (2.3) for the three cases above, and in fact, for any form of $\delta(x)$ as defined in (2.1). The probability that a female finds one or more mates takes a negative exponential (hereafter NE) form:

$$(2.12) \qquad\qquad \Pr[X(a) \geq 1] = 1 - e^{-\beta n},$$

where $\beta = ab$. The quantity $1/\beta$ is the population density at which the probability of mating is $1 - e^{-1} \approx 0.632$. The expected number of females that mate, and presumably reproduce, is then proportional to $n(1 - e^{-\beta n})$. Philip [1957] was the first to utilize (2.12) as an Allee effect in a dynamic growth model (see §3). Southwood and Comins [1976] later employed (2.12) in their "synoptic" population model, and Gerritsen [1980] incorporated (2.12) in a Leslie matrix model. The above derivation shows the NE function is a general expression valid for a variety of spatial patterns.

An NE function, in fact, is an encounter *frequency* as well as an encounter *probability*. The expected encounter frequency for a given female is (2.11) if Case 3 is applicable. This interpretation of the NE encounter function is preferable when a female reproduces at a greater rate with increased number of copulations. In the spirit of Volterra's model, the expected number of meetings between the sexes (and consequently the expected reproductive rate) is proportional to $n(1 - e^{-\beta n})$ (where $\beta = -ac$) instead of n^2.

The RH Function. What if the population is not homogeneous with regard to the value of β? For instance, β might vary between

individuals due to differences in the distances traversed (Gerritsen and Strickler [1977], Gerritsen [1978]) sizes of home ranges, factors affecting pheremone diffusion (Scott [1973]) or attractiveness (Bobb [1972]), or other random environmental factors. A continuous probability distribution, with an associated probability density function $f(\beta)$, could then represent the heterogeneity in β values. An individual picked at random from the population would constitute a sample value from that distribution.

The NE function (2.12) is a probability conditioned on a fixed value of β. The unconditional probability of mating (i.e., for a randomly selected female) is the average of (2.12) over all possible β values:

$$\Pr[X(a) \geq 1(\text{unconditional})] = \int_0^\infty (1 - e^{-\beta n})f(\beta)d\beta$$

(2.13)

$$= 1 - \int_0^\infty e^{-\beta n}f(\beta)d\beta = 1 - \phi(n).$$

The function $\phi(n)$ is seen to be the Laplace tranform of $f(\beta)$. It is also the probability that a randomly selected female does not encounter a mate in a population of density n. That the Laplace transform of a probability distribution might itself be interpreted as a probability is well known (e.g., Rade [1972]).

One candidate probability density function for the form of $f(\beta)$ is that of the exponential distribution (not to be confused with the NE encounter function):

(2.14) $$f(\beta) = \theta e^{-\theta\beta}, \quad 0 < \beta < \infty.$$

The parameter θ is positive; the mean of the distribution is $1/\theta$. Use of this distribution does not entail a net increase of the number of parameters, as β is integrated out of the mating probability (2.13). The exponential is the "most random" of the probability distributions with ranges 0 to ∞ and finite means (in the sense of having minimal information content — see Shannon and Weaver [1964]). It is simple and yet representative of a wide variety of stochastic phenomena. Owen et al. [1973], for example, incorporate (2.14) into butterfly mating frequency studies as an age distribution.

The unconditional probability of mating under the exponential distribution is, from (2.13) and (2.14),

(2.15) $$\Pr[X(a) \geq 1] = 1 - \phi(n) = n/(\theta + n).$$

The function is a rectangular hyperbola (hereafter RH) in n; θ is the population density at which the probability of mating is $1/2$. Ecologists have often used such a function to describe the limitation of the growth rate of an organism by its food supply (in which case n in this function would be the food supply — see Williams [1980], Holling [1965]). In the present context the RH (2.15) describes the limitation of the reproductive rate of an organism by the sheer paucity of its own species (§3 and §4).

The RH as a fertilization probability was introduced by Kostitzin ([1940], a translation appears in Scudo and Ziegler [1978]). He supposed that the number of "favorable chances" for fertilization would be proportional to n, whereas the number of "unfavorable chances" would be a constant, θ. While this underlying chance mechanism is vague, Kostitzin's primary purpose was to modify Volterra's BC model to produce reasonable behavior for all population densities. Hopf and Hopf [1985] used a similar hyperbolic function as an Allee effect in multiple species competition models.

The expected encounter frequency, in addition to the probability of encounter, is an RH function if the Case 3 model (2.11) is applicable and the parameter a (or β) has an exponential distribution. The RH function can then be incorporated as a satiation effect into Volterra's collision model, thus providing an underlying basis for Kostitzin's use of the RH function. The number of encounters between the sexes here becomes proportional to $n^2/(\theta + n)$ instead of n^2.

Curiously, the RH encounter function arises in an entirely different context as a model of an insect pest control method. Sterile males are released and maintained at a density of γ within the pest population under this method. If the density of wild males is νn, the probability that a female mates with a fertile (wild) male is $n/[(\gamma/\nu) + n]$. Some assumptions are: (1) the sterile males are as vigorous as fertile males, (2) the sex ratio remains constant, and (3) the organisms have no trouble finding each other. This model originated with Knipling [1955] and is extended by Lawson [1967] and Costello and Taylor [1975]. Interestingly, Kostitzin's chance mechanism seems to describe the sterile male technique more appropriately than it does mating encounter limitation. Subsequent discussions of dynamic growth models containing the RH mating encounter function (§3 and §4) apply readily to models containing the sterile male function.

The RH function, compared to the NE function, tends to approach the asymptote less quickly (see Figure 1). The shape differences of these curves are slight enough, though, so that in practice these curves often describe biological data equally well. Indeed, the NE and the RH are usually statistically indistinguishable in their applications to feeding rate studies (e.g., Mullin et al. [1975]). I prefer the RH purely for mathematical convenience. Even the simplest dynamical population growth models incorporating the NE can be quite intractable (§3 and §4).

Other encounter functions. Virtually any continuous probability distribution specified as the form for $f(\beta)$ in (2.13) will yield an encounter probability curve, $1 - \phi(n)$, shaped similarly to the two curves in Figure 1. In particular, the encounter probability will not be sigmoid (s-shaped) if $f(\beta)$ does not depend on n. Note that the second derivative of $\phi(n)$ is

$$(2.16) \qquad \phi''(n) = \int_0^\infty \beta^2 e^{-n\beta} f(\beta) d\beta$$

for $n > 0$. If the variance of the distribution $f(\beta)$ exists, then $\phi''(n)$ is defined for $n = 0$ as well. Since the integrand $\beta^2 e^{-n\beta} f(\beta)$ is never less than zero in the range of the integral, $\phi''(n) \geq 0$, implying that $1 - \phi(n)$ is concave, or in particular, has no inflection points. This property is a special case of the completely monotone property of Laplace transforms of probability distributions (see Feller [1966, p. 415]).

As an example, a possible form for $f(\beta)$ is the gamma density:

$$(2.17) \qquad f(\beta) = \theta^\tau \beta^{\tau-1} e^{-\theta\beta}/\Gamma(\tau), \quad 0 < \beta < \infty,$$

where $\Gamma(\cdot)$ is the gamma function, and τ, θ are positive parameters. The distribution is very flexible and can approximate many data sets (the exponential distribution (2.14) is a special case when $\tau = 1$). Alternatively, a more mechanistic formulation of the mating process might lead to the Raleigh distribution with density

$$(2.18) \qquad f(\beta) = (\beta/\sigma^2) e^{-\beta^2/(2\sigma^2)}, \quad 0 < \beta < \infty,$$

where σ^2 is a positive parameter. The Raleigh distribution describes the distance a randomly diffusing particle travels from its starting

point (Skellam [1952], Pielou [1977, p. 172]). The distribution could represent the spread of a pheremone (see Bossert and Wilson [1963]), the release of gametes into the environment, or the sorties of an organism from a fixed location (as in Siniff and Jessen [1969]).

When the Laplace transforms of (2.17) and (2.18) are obtained, the mating probabilities are found to be

(2.19) (gamma) $1 - \phi(n) = [(\theta + n)^\tau - \theta^\tau]/(\theta + n)^\tau$;

(2.20) (Raleigh) $1 - \phi(n) = [1 - \mathrm{erf}(\sigma n/\sqrt{2})]\sigma n\sqrt{(\pi/2)}\,e^{\sigma^2 n^2/2}$.

Here $\mathrm{erf}(z)$ is the error function representing the area under the standard normal curve between $2z$ and $-2z$ (see Abramowitz and Stegun [1965, p. 297]). The curves (2.19) and (2.20) resemble the RH and the NE mating curves in shape. In fact, letting $\tau \to \infty, \theta \to \infty$ such that $\tau/\theta \to \beta$ in (2.19) retrieves the NE model (2.12) in the limit, and, as noted earlier, $\tau = 1$ recovers the RH model. However, a computer is needed to solve the dynamic growth models in §3 and §4 if mating functions such as (2.19) and (2.20) are utilized. The RH, by contrast, permits rather simple mathematical analysis.

Data analysis. The RH and NE functions fit an existing data set reasonably well (Figure 1). The data are from Nishigaki [1963], who recorded copulation frequencies of newly emerged azuki bean weevils at various population densities in laboratory experiments. I obtained parameter estimates by the maximum likelihood method using a product binomial likelihood function (see Dennis [1982] for details of the iterative calculations necessary). The appropriate estimation approach is similar to that of dose-response studies. The dependent variable is a binary response (mated or unmated) of each female at a given density ("dose") of males. A likelihood ratio goodness-of-fit test was derived for these mating models (Dennis [1982]). Both models fit quite well according to this test (NE: pr = 0.30; RH: pr = 0.79). However, a superior fit for the NE is evident by inspection of the graph (Figure 1). The RH appears to systematically over-predict the mating frequencies at low population densities and under-predict the frequencies at high densities. Both curves adequately describe the general shape of the response, though, given the variability of binary data.

There are two potential approaches to estimating parameters for these mating functions. One approach is to fit the curves directly to data sets
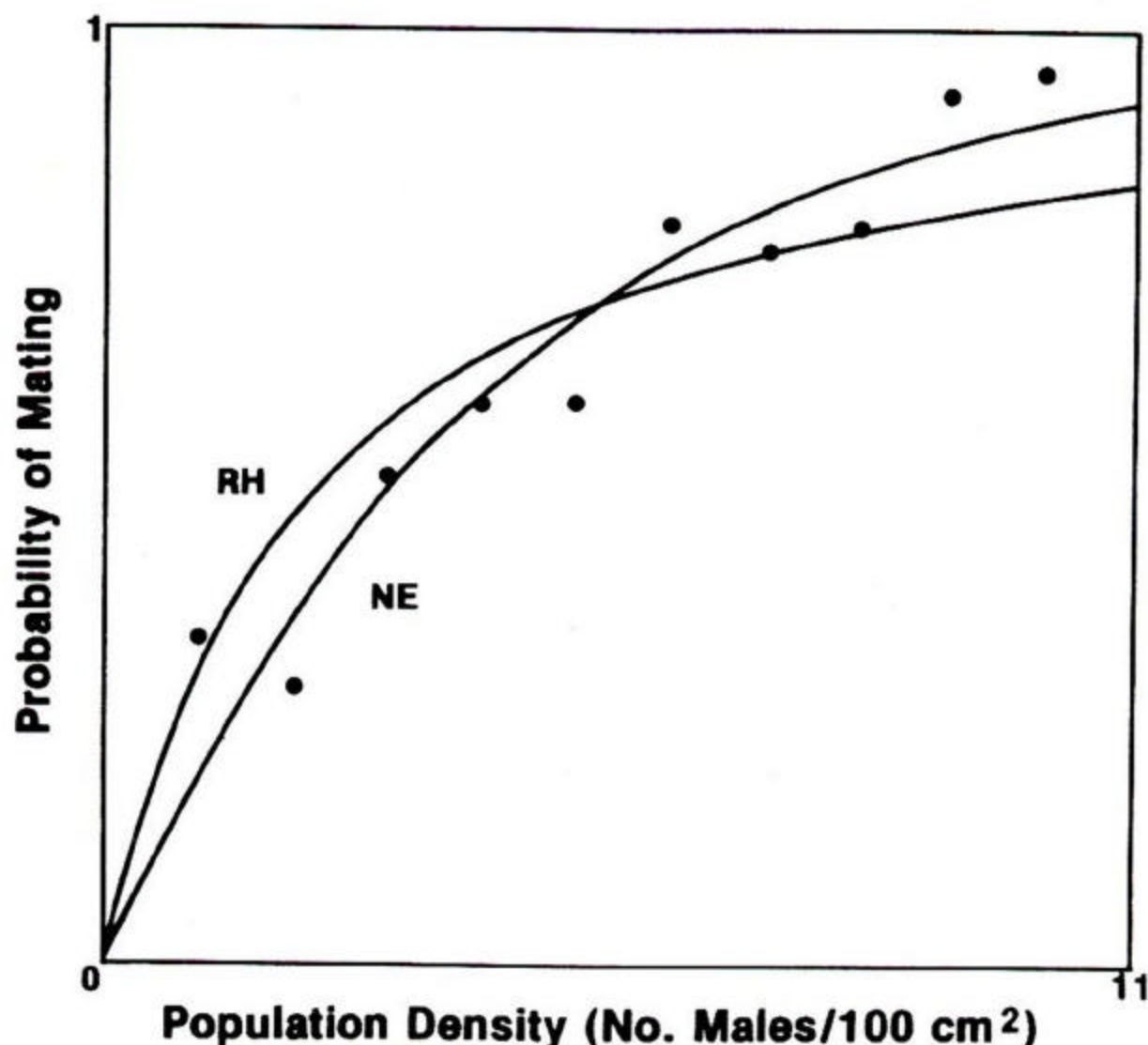
FIGURE 1. Estimated RH and NE encounter functions, $n/(\theta + n)$ and $1 - e^{-\beta n}$, plotted with observed mating frequencies of azuki bean weevils. Data are from Nishigaki [1963]. Maximum likelihood parameter estimates are: (RH) $\theta = 2.156$, (NE) $\beta = 0.2360$.

involving the percent females which have mated (or percent which are pregnant or display reproductive evidence such as litters, recent placental scars, etc.) at different population densities. This approach was illustrated above using the Nishigaki [1963] data. A second approach is to estimate the parameters directly from movement data or mating behavior studies. For instance, Mosimann [1958] utilized Stickel's [1950] data on box turtle movements and obtained estimates of encounter probabilities with the NE function. Gerritsen and Strickler [1977] and Gerritsen [1980] computed encounter probabilities based on

zooplankton swimming velocities and sensory detection distances. Jorgensen [1968] presented a technique for estimating probabilities of interaction and home ranges using recapture data on small mammals. Radio telemetry studies might potentially contribute greatly to encounter rate investigations.

3. Deterministic growth. Single species population growth models are often of the form

$$(3.1) \qquad\qquad dn/dt = \lambda(n) - \mu(n),$$

where n = population density, $\lambda(n)$ = rate of births in the population, and $\mu(n)$ = rate of deaths in the population. These models assume: (1) population density is adequately characterized by a continuous function of time, $n(t)$, (2) the individual members of the population are homogeneous in their impacts on the rate of change of $n(t)$, and (3) $\lambda(\cdot)$ and $\mu(\cdot)$ are homogeneous in time and space.

This section considers models of population growth of the form (3.1). The section first incorporates the mating encounter functions from §2 into the birth rate term, $\lambda(n)$. In particular, the NE and the RH functions are used, the NE because of its biological generality, and the RH due to its mathematical tractability. A simple linear birth rate is used as a null hypothesis against which to test the birth rates containing Allee effects. A BC birth rate is also treated in this section, since it possesses some of the qualitative properties of the more realistic NE and RH birth rates. The section then thoroughly analyzes various deterministic population growth models containing these birth rates. Pure birth models, for situations where mortality is insignificant, are examined first. Birth-death models are then developed; a property of these models is a critical density, or lower unstable equilibrium. Next, this section incorporates mating functions into population models having an upper stable equilibrium. The section closes with a study of how harvesting amplifies Allee effects.

Mating encounters and birth rates. A copulation shortage would affect the birth rate term in (3.1). The encounter frequency models of §2 permit construction of several forms for $\lambda(n)$ (see Table 1).

TABLE 1.

Forms of the birth rate, $\lambda(n)$, for the SL, BC, NE, and RH models

$$
\lambda(n) = \begin{cases} \text{(i)} & \lambda n & \text{simple linear (SL)} & \rbrace \text{ (non-mating)} \\ \text{(ii)} & \lambda\alpha n^2 & \text{bimolecular collisions (BC)} \\ \text{(iii)} & \lambda n(1 - e^{-\beta n}) & \text{negative exponential (NE)} & \Big\rbrace \quad \text{(mating} \\ \text{(iv)} & \lambda n^2/(\theta + n) & \text{rectangular hyperbola(RH)} & \text{limited)} \end{cases}
$$

(i) The simple linear (hereafter abbreviated SL) birth rate does not account for mating encounters (SL, Table 1). The assumption is that $\lambda(n)$ is merely proportional to n when matings are frequent enough so as not to limit reproduction. Models with the SL birth rate appear often in ecological applications, and will here represent the null hypotheses against which the models containing Allee effects may be tested.

(ii) The simplest birth rate incorporating some form of mating limitation (BC, Table 1) assumes reproduction to be proportional to the frequency of bimolecular collisions between the sexes. The BC birth rate includes a separate proportionality constant, α, so that λ is the same quantity in the BC and the SL rates. The BC rate does mimic one expected feature of an Allee effect: the per-individual birth rate, $\lambda(n)/n$, is an increasing function of n (Figure 2). However, the BC rate exceeds the basic SL rate for higher population densities. This undesirable property suggests that BC growth models, if used at all, should be constrained to describing populations only at low densities.

(iii) The NE birth rate incorporates mating limitation in the form of the NE encounter function (NE, Table 1). The reproductive rate is here proportional to the expected number of females mating one or more times under the assumptions discussed in §2. Alternatively, $n(1-e^{-\beta n})$ represents the expected frequency of copulations in a population under satiation assumptions of §2. The per-individual NE birth rate is an increasing function of n, but it asymptotically approaches that of the SL rate as n becomes large (Figure 2).

(iv) The RH encounter function is utilized for mating limitation in the fourth birth rate (RH, Table 1). As in the NE birth rate, the RH rate uses the encounter function as either an encounter probability or an encounter frequency. Population growth models incorporating the RH rate invariably have dynamical behavior similar to those models using

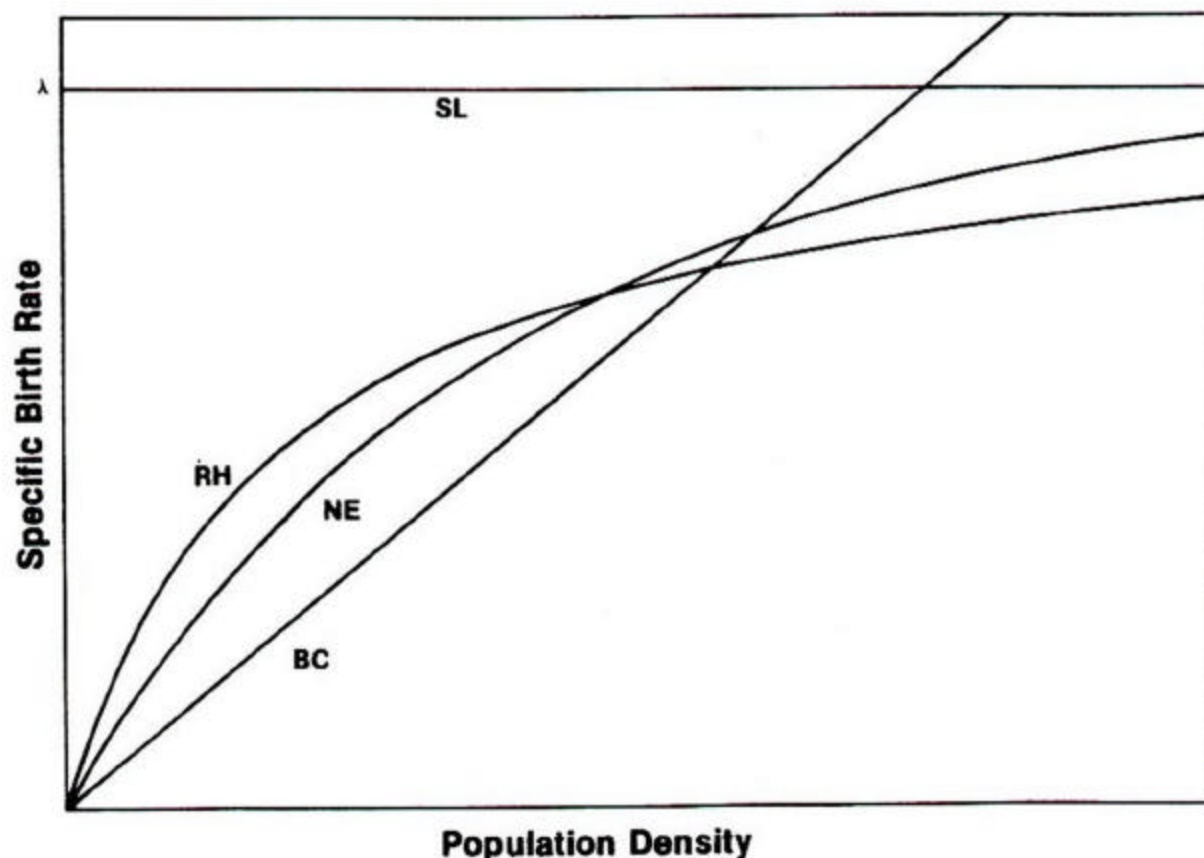the NE rate, as is clear from comparing the RH and NE per-individual birth rates (Figure 2).

FIGURE 2. The per-individual birth rates, $\lambda(n)/n$, plotted as functions of population density, n, for the SL, BC, NE, and RH models. Table 1 lists the functional forms for $\lambda(n)$.

Data analysis. Nishigaki [1963] collected data on reproductive rates resulting from the azuki bean weevil mating experiments discussed in §2. For each of the population densities, he recorded the number of: (1) eggs hatched per female, and (2) eggs hatched per mated female. The RH and NE curves are nearly indistinguishable when fit to the data on number of eggs per female (Figure 3). Parameters here are estimated through nonlinear regression, since the dependent variable is continuous, not binary as was the example in §2. For the RH model, the asymptotic normal distribution of the estimate of θ may be used in a statistical test of the hypothesis $H_0 : \theta = 0$ vs. the hypothesis $H_1 : \theta > 0$. The test rejects H_0, the SL model, in favor of H_1, the RH model (pr $= 0.01$), for the data in Figure 3.
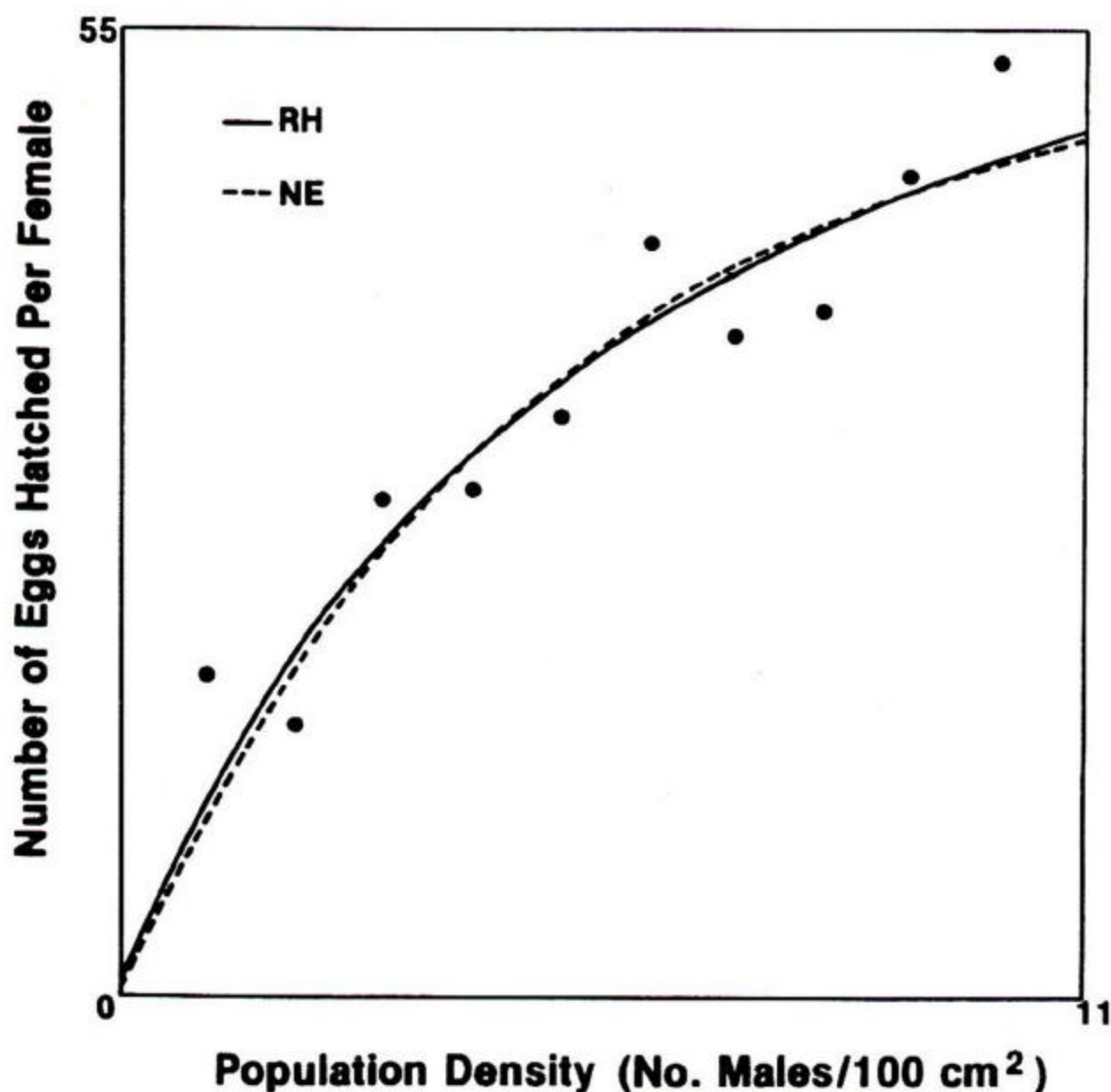
FIGURE 3. Estimated RH and NE birth rates plotted with observed
number of eggs hatched per female bean weevil. Data are from Nishigaki
[1963]. Nonlinear least squares estimates are: (RH) $\theta = 5.767$, $\lambda = 75.28$.
(NE) $\beta = 0.2086$, $\lambda = 54.24$.

The SL model provides a good description of Nishigaki's data on
the number of eggs per *mated* female (Figure 4). This would be the
expected model if the females had no trouble finding mates. The
parameter estimate for λ is simply the sample mean of the observations
on the dependent variable.

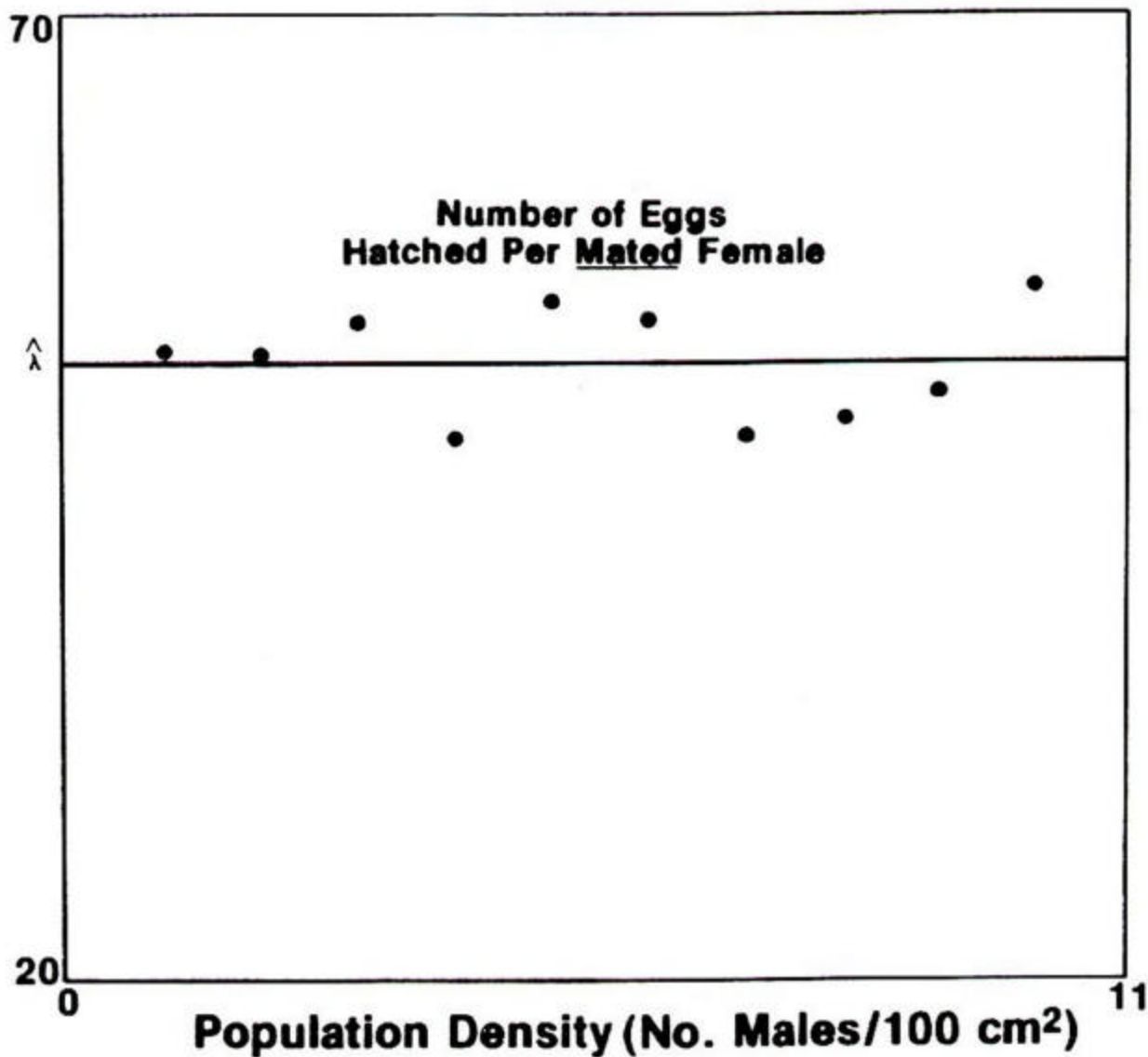*Pure birth models.* A pure birth model may be appropriate if

FIGURE 4. Estimated SL birth rate plotted with observed number of eggs per mated female bean weevil. Data are from Nishigaki [1963]. Here $\lambda = 51.94$.

mortality losses are insignificant. Such a model sets $\mu(n) = 0$ in (3.1). Integration of (3.1) explicitly gives the time, t, required for a population of initial size m to reach a given larger size n :

$$(3.2) \qquad \int_m^n [1/\lambda(v)]\, dv = t.$$

Equation (3.2) yields an explicit solution for n in terms of m and t for only some birth rates.

(i) The waiting time to reach size n for the SL model is, from (3.2),

$$(3.3) \qquad t = (1/\lambda)[\log n - \log m].$$

Equation (3.3) of course may be rearranged to give the more familiar expression for exponential growth:

$$(3.4) \qquad n = me^{\lambda t}.$$

(ii) The waiting time for the BC model approaches a constant, $1/(m\lambda\alpha)$, as $n \to \infty$:

$$(3.5) \qquad t = [1/(\lambda\alpha)][(1/m) - (1/n)].$$

This means the solution trajectory for the BC birth model is explosive: n becomes infinite in a finite time. A population's growth could thus be approximated by this model only for short time periods and low initial densities.

(iii) The integral (3.2) for the NE model is an infinite series:

$$(3.6) \quad t = (1/\lambda)[\log n - \log m] + (1/\lambda)\sum_{k=1}^{\infty}[\mathrm{Ei}(-k\beta n) - \mathrm{Ei}(-k\beta m)].$$

Here $\mathrm{Ei}(\cdot)$ is the exponential-integral function (see Gradshteyn and Ryzhik [1965, p. 925]). The expression (3.6) follows from (3.2) by noting: (a) $1/(1 - e^{-\beta n}) = 1/(1 - q) = 1 + q + q^2 + \ldots$, and (b) $\int(e^{sx}/x)\,dx = \mathrm{Ei}(sx) + \text{constant}$ (Gradshteyn and Ryzhik [1965, p. 93]). It is seen that the NE waiting time (3.6) exceeds the SL waiting time (3.3) by an amount depending on the parameter β.

(iv) The reciprocal of the RH birth rate, $1/\lambda(n)$, is the sum of an "SL component," $1/(\lambda n)$, and a "BC component," $\theta/(\lambda n^2)$. The waiting time resulting from (3.2) thus contains a term resembling (3.3) and a term resembling (3.5):

$$(3.7) \qquad t = (1/\lambda)[\log n - \log m] + (\theta/\lambda)[(1/m) - (1/n)].$$

Note that (3.7) is a linear function of θ.

Population growth at low initial densities under the RH and NE birth models is sluggish compared to the non-mating SL model. The waiting

times to reach size n are greater in the two mating models by amounts that depend on the parameters θ and β. Recall that these parameters are related to the mate finding abilities of the population members. As θ increases or β decreases, the mating rate decreases, and the waiting time increases. Also, (3.7) and (3.6) begin to resemble exponential growth (3.3) for large initial densities.

Birth-death models. The events of population decline and extinction become important when mortality losses are significant. For simplicity, a constant per-individual death rate is assumed, so $\mu(n) = \mu n$ in (3.1). Equation (3.1) is readily solved for the waiting time to reach size n :

$$(3.8) \qquad \int_m^n \{1/[\lambda(v) - \mu(v)]\}\, dv = t.$$

A positive equilibrium, $\bar{n}$, will typically exist in the encounter-limited models where $\lambda(\bar{n}) = \mu\bar{n}$. This equilibrium is given by

$$(3.9) \qquad \bar{n} = h^{-1}(\mu),$$

where $h(n) = \lambda(n)/n$ is the per-individual birth rate (an increasing function of n). The equilibrium is unstable, that is, the population increases if $m > \bar{n}$ and decreases to extinction if $m < \bar{n}$. This is shown by noting that $h'(n) > 0$ by definition and $\lambda'(n) = h(n) + nh'(n)$. The stability of the equilibrium (3.9) depends on the sign of the (single) eigenvalue in the linear approximation to $dn/dt = \lambda(n) - \mu n$ near $\bar{n}$. That eigenvalue is $\partial(dn/dt)/\partial n$ evaluated at $\bar{n}$:

$$(3.10) \qquad \begin{aligned} \partial(dn/dt)/\partial n\Big|_{\bar{n}} &= \lambda'(\bar{n}) - \mu \\ &= h(h^{-1}(\mu)) + \bar{n}h'(\bar{n}) - \mu \\ &= \mu + \bar{n}h'(\bar{n}) - \mu = \bar{n}h'(\bar{n}) > 0. \end{aligned}$$

The positive sign indicates that solution trajectories near $\bar{n}$ deviate away from $\bar{n}$; in other words, $\bar{n}$ is locally unstable. Mating encounters are just sufficient to compensate for deaths at the point $\bar{n}$. I term this equilibrium the *critical density.*

(i) From (3.8) we have

$$(3.11) \qquad t = [1/(\lambda - \mu)] \log(n/m)$$

if the organisms have no trouble finding each other. Under this SL model the population grows exponentially ($n = me^{(\lambda-\mu)t}$), assuming $\lambda > \mu$.

(ii) Volterra [1938] proposed the BC birth-death model. The solution in terms of the waiting time is

(3.12) $t = (1/\mu)\{\log[(n-\bar{n})/(m-\bar{n})] - \log(n/m)\},$

or in terms of n is

(3.13) $n = \bar{n}/\{1 + [(\bar{n}-m)/m]e^{\mu t}\}.$

Here the critical density is $\bar{n} = \mu/(\lambda\alpha)$. The model could only describe population growth for short time intervals if $m > \bar{n}$, as the solution trajectories explode toward infinity at time $t = -(1/\mu)\log[1 - (\bar{n}/m)]$.

(iii) The critical density for the NE model is $\bar{n} = -(1/\beta)\log[1 - (\mu/\lambda)]$. If $n > m > \bar{n}$ the waiting time solution is

$$t = [1/(\lambda-\mu)]\log(n/m)$$
(3.14)
$$+ [1/(\lambda-\mu)]\sum_{k=1}^{\infty}[\lambda/(\lambda-\mu)]^k[\mathrm{Ei}\,(-k\beta n) - \mathrm{Ei}\,(-k\beta m)].$$

If $n < m < \bar{n}$ the solution is

(3.15) $t = [1/(\lambda-\mu)]\sum_{k=1}^{\infty}[(\lambda-\mu)/\lambda]^k[\mathrm{Ei}\,(k\beta m) - \mathrm{Ei}\,(k\beta n)].$

These expressions are obtained by expanding the integrand of (3.8), or $1/[\lambda n(1 - e^{-\beta n}) - \mu n]$, in a geometric power series. If $m > \bar{n}$, then the integrand can be written as $1/[(\lambda-\mu)n(1-q)] = [1/(\lambda n - \mu n)](1 + q + q^2 + \ldots)$, where $q = [\lambda/(\lambda-\mu)]e^{-\beta n}$. If $m < \bar{n}$, then the integrand becomes $-[e^{\beta n}/(\lambda n)][1/(1-r)] = -[e^{\beta n}/(\lambda n)][1 + r + r^2 + \ldots]$, where $r = [(\lambda-\mu)/\lambda]e^{\beta n}$. These expressions, despite being analytical solutions to the NE birth-death model, are not very useful computationally.

(iv) The critical density for the RH model is $\bar{n} = \theta\mu/(\lambda-\mu)$. The waiting time solution contains a term resembling the SL model (3.11)

and a term resembling the BC model (3.12), when $n > m > \bar{n}$ or $n < m < \bar{n}$:

$$(3.16) \quad t = [1/(\lambda - \mu)] \log(n/m) \\ + [(\lambda/\mu)/(\lambda - \mu)]\{\log[(n - \bar{n})/(m - \bar{n})] - \log(n/m)\}.$$

In neither the RH model nor the NE model does the population become infinite in finite time. Instead, the trajectories tend to resemble exponential growth (SL) for large population densities. Population increase is slow when m is near, but greater than, $\bar{n}$; note how the waiting times (3.14) and (3.16) are increased over the SL model (3.11). Plots of the RH solution (3.16) for various initial densities illustrate the decline of the population toward extinction when $m < \bar{n}$ (Figure 5; NE plots are similar).
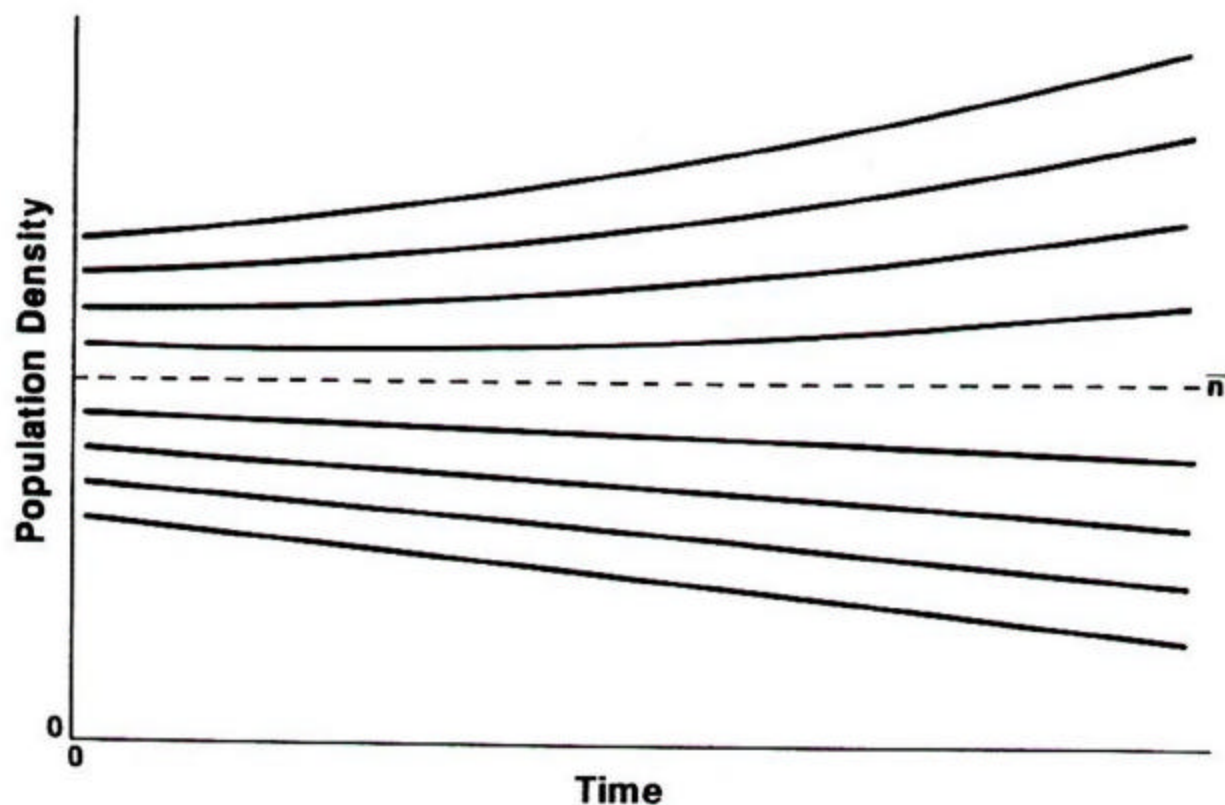

FIGURE 5. Population density, n, graphed as a function of time, t, for the RH birth-death model (3.16). The critical density is $\bar{n}$.

The critical density is proportional to θ in the RH model and $1/\beta$ in the NE model. To reiterate, both quantities are in units of population density and are inverse measures of mate finding ability (§2).

Upper limit to population growth. Growth above critical density continues indefinitely under the preceding models. Such models might represent populations during chronic or recurring periods at low density, or colonizing species during early phases of growth. These models can be generalized to higher densities by incorporating an upper limit to population growth, for purposes of, say, studying reduction of abundant populations through harvesting, habitat removal, or biological control.

(i) An important single species model of population limitation is the logistic equation. Hutchinson [1978] and Kingsland [1985] provide thorough ecological and historical reviews of this model. The model plays a significant role in the theory of managing renewable resources (Miller and Botkin [1974], Clark [1976], Brauer and Sanchez [1975], May et al. [1979]). The central assumption of the logistic is that the difference of the per-individual birth and death rates is a linear declining function of n :

(3.17) $(1/n)dn/dt = [\lambda(n) - \mu(n)]/n = r - (r/k)n.$

Integrated forms of (3.17) are:

(3.18) $t = (1/r)\{\log(n/m) - \log[(n - k)/(m - k)]\};$
(3.19) $n = k/\{1 + [(k - m)/m]e^{-rt}\}.$

The logistic is a descriptive model purporting to approximate many models with more realistic assumptions. Consider a growth model of the general form

(3.20) $dn/dt = ng(n),$

where $g(n)$ is the per-individual growth rate. An equilibrium, $\bar{n}$, will be a root of

(3.21) $g(\bar{n}) = 0.$

Furthermore,

(3.22) $g'(\bar{n}) < 0$

gives the criterion for local stability of that equilibrium. Expanding $g(n)$ in a Taylor series about $\bar{n}$ gives the logistic approximation to (3.20):

$$
\begin{aligned}
dn/dt &= n[g(\bar{n}) + (n - \bar{n})g'(\bar{n}) + \cdots] \\
&\approx \bar{n}[-g'(\bar{n})]n + [g'(\bar{n})]n^2 \\
&= rn - (r/k)n^2,
\end{aligned}
$$

(3.23)

where $r = -\bar{n}g'(\bar{n})$, $k = \bar{n}$. This derivation is emphasized here because the usual presentation in the ecological literature expands $ng(n)$ around *zero*, which obtains a value of k *not equal to*, in general, the true equilibrium $\bar{n}$.

(ii) Volterra [1938] noted the similarity of (3.19) to the earlier BC birth-death model (3.13). The per-individual growth rates for both are linear functions of n. The slope $(\lambda\alpha)$ of the linear per-individual growth rate in the mating model is positive, though, and the intercept $(-\mu)$ is negative. Volterra tamed the consequent explosive trajectories of (3.13) by subtracting a quadratic term from the per-individual growth rate:

(3.24)
$$
(1/n)dn/dt = -\mu + \lambda\alpha n - \gamma n^2.
$$

He reasoned that the birth parameter λ in the BC birth rate might be expected to decline linearly with n. Then $\lambda(n)$ becomes $(\lambda\alpha n - \gamma n^2)n$, and $\mu(n) = \mu n$ as before. The integrated form of (3.24) is

(3.25)
$$
\begin{aligned}
t = (1/\mu)\{&[\bar{n}_2/(\bar{n}_2 - \bar{n}_1)]\log[(n - \bar{n}_1)/(m - \bar{n}_1)] \\
&- [\bar{n}_1/(\bar{n}_2 - \bar{n}_1)]\log[(n - \bar{n}_2)/(m - \bar{n}_2)] - \log(n/m)\},
\end{aligned}
$$

where

(3.26) $$\bar{n}_1 = \{\lambda\alpha - [(\lambda\alpha)^2 - 4\mu\gamma]^{1/2}\}/(2\mu),$$
(3.27) $$\bar{n}_2 = \{\lambda\alpha + [(\lambda\alpha)^2 - 4\mu\gamma]^{1/2}\}/(2\mu).$$

The quantities $\bar{n}_1$ and $\bar{n}_2$ are equilibria; $\bar{n}_1$ is unstable (lower critical density), and $\bar{n}_2$ is stable. Thus, the population reaches a high steady-state value $\bar{n}_2$ if $m > \bar{n}_1$, whereas the population faces extinction if $m < \bar{n}_1$.

(iii), (iv) The logistic model accommodates the RH or NE encounter functions in the following manner. If $n/(\theta + n)$ is the probability of

mating, using the RH function as an example, then $1 - n/(\theta + n) = \theta/(\theta + n)$ is the probability of not mating. One may subtract a term proportional to $\theta/(\theta + n)$ from the per-individual growth rate in (3.17) to represent the reduction of reproduction due to mating shortage. We then have the logistic model adjusted for mating encounters:

$$(3.28) \qquad dn/dt = rn - (r/k)n^2 - \lambda\theta n/(\theta + n).$$

Kostitizin [1940] briefly mentioned the growth model (3.28), and Dennis [1982] and Jacobs [1984] examined its behavior. Similar equations received attention as models of populations growing logistically but suffering harvesting or predation in the form of some functional response (Brauer [1979], Ludwig et al. [1978], Huberman [1978], May, [1977b]). Philip [1957] presented the version of (3.28) using the NE mating function (see also Elseth and Baumgardner [1981, p. 343]). Equation (3.28) is dynamically similar to Philip's model, though (3.28) integrates more easily. The waiting time solution resembles (3.25):

$$(3.29) \quad t = [1/(\lambda - r)]\{[\bar{n}_2(\bar{n}_1 - \theta)/(\theta(\bar{n}_2 - \bar{n}_1))] \log[(n - \bar{n}_1)/(m - \bar{n}_1)]$$
$$- [\bar{n}_1(\bar{n}_2 - \theta)/(\theta(\bar{n}_2 - \bar{n}_1))] \log[(n - \bar{n}_2)/(m - \bar{n}_2)] - \log(n/m)\},$$

where

$$(3.30) \qquad \bar{n}_1 = \{-B + [B^2 - 4AC]^{1/2}\}/(2A),$$
$$(3.31) \qquad \bar{n}_2 = \{-B - [B^2 - 4AC]^{1/2}\}/(2A),$$

with $A = -r/k, B = r(1 - \theta/k)$, and $C = \theta(r - \lambda)$. The critical density is $\bar{n}_1$; the upper steady-state density is $\bar{n}_2$. Solution (3.29) graphed for various values of m shows the critical density and the upper stable density (Figure 6).

A diagram of the k-n plane, displayed by Philip [1957] for the NE version of the logistic, allows examination of the behavior of (3.29) for different values of k (Figure 7). The curves of the equilibria $\bar{n}_1$ and $\bar{n}_2$ divide the plane into four regions of increase or decline. The diagram contains important implications for wildlife management strategies. Traditional management techniques are often based on habitat manipulation (Allen [1962, p. 61]). We might presume such techniques have the effect of adjusting the parameter k in the model. An increased k would be expected to yield an increased steady-state population if
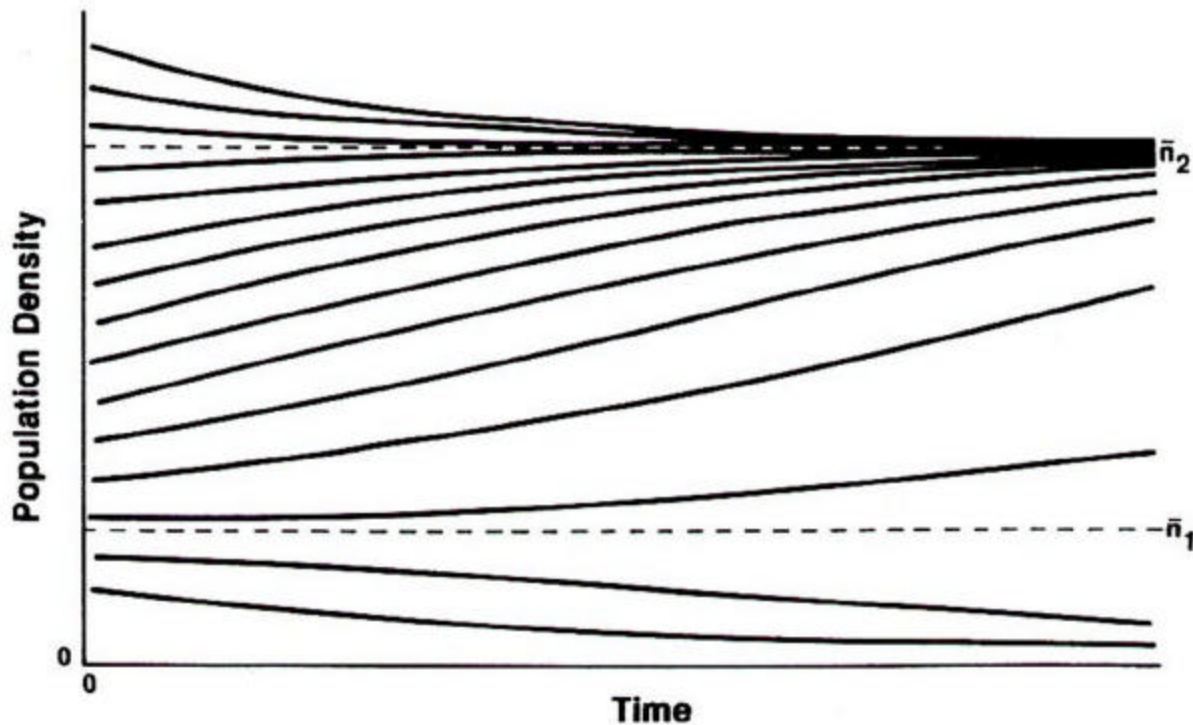
FIGURE 6. Population density, n, graphed as a function of time, t, for the RH-logistic model (3.28). Equilibria occur at $\bar{n}_1$ (unstable) and $\bar{n}_2$ (stable).

the population is in regions 3 and 4, in agreement with classical wildlife theory. Considerable increases in k might be futile toward saving an endangered population, however, if the population is in region 2. Management measures directly increasing reproduction, density, or survival (e.g., captive breeding, transporting animals, breeding ground or nest site protection) would be more effective for populations experiencing Allee effects.

Harvesting. Simple assumptions can extend the previous growth models to account for population losses through harvesting. One type of model, known as a "constant effort" harvesting model, assumes the population suffers losses at an instantaneous rate En. The quantity E is a measure of harvesting effort, based perhaps on the number of boats, number of hunters, or type of gear, and is assumed constant through time. Another type known as a "constant rate" harvesting model simply assumes the instantaneous loss rate due to harvesting is a constant, E. Clark [1976] discusses these and other harvesting assumptions.
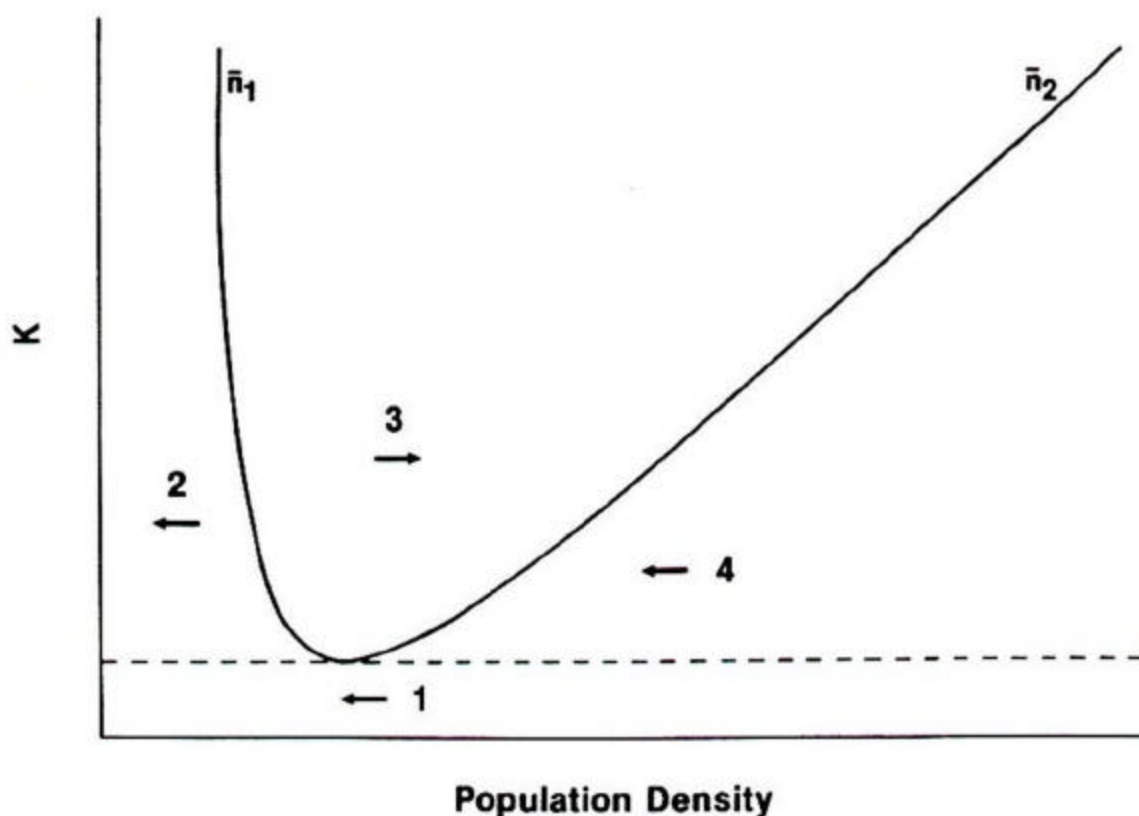
Population Density

FIGURE 7. Equilibria of the RH-logistic, (3.30) and (3.31), divide the k-n plane into four regions. (1) Population declines to extinction. (2) Population declines to extinction. (3) Population increases to $\bar{n}_2$. (4) Population decreases to $\bar{n}_2$.

With constant effort harvesting, a population model such as (3.20) becomes

$$(3.32) \qquad dn/dt = ng(n) - En.$$

An equilibrium, $\hat{n}$, of a harvested population is now a root of

$$(3.33) \qquad g(\hat{n}) - E = 0.$$

The effect of such harvesting is to decrease locally a stable equilibrium and increase an unstable one. To see this, recall that an equilibrium, $\bar{n}$, of an unharvested population is a root of (3.21), with (3.22) giving the criterion for local stability. Near $\bar{n}$, $g(\hat{n}) \approx -\bar{n}g'(\bar{n}) + \hat{n}g'(\bar{n})$ by Taylor series approximation. Substituting the approximation for $g(\hat{n})$ in (3.33) gives

$$(3.34) \qquad \hat{n} \approx \bar{n} + E/g'(\bar{n}).$$

The harvested equilibrium $\hat{n}$ is locally greater than or less than $\bar{n}$ depending on the sign of $g'(\bar{n})$.

Encounter limitation in the absence of an upper stable equilibrium has an effect similar to constant rate harvesting. Under constant rate harvesting, the instantaneous harvest rate does not depend on n:

$$(3.35) \qquad dn/dt = ng(n) - E.$$

Consider now an SL birth-death model harvested at a constant rate $\mu\theta$. In other words,

$$(3.36) \qquad dn/dt = \lambda n - \mu n - \mu\theta.$$

The equilibrium (unstable) for this model is

$$(3.37) \qquad \hat{n} = \theta\mu/(\lambda - \mu),$$

identical to the critical density equilibrium from the RH birth-death model (see discussion preceding (3.16)).

The logistic model (3.17) with constant effort harvesting is known in the fisheries literature as the Schaefer model (after Schaefer [1957]):

$$(3.38) \qquad dn/dt = rn - (r/k)n^2 - En.$$

The integrated form is

$$(3.39) \qquad n = (k - kE/r)/\{1 + [(k - kE/r - m)/m]e^{-(r-E)t}\},$$

or just a logistic equation with an equilibrium at

$$(3.40) \qquad \hat{n} = k(1 - E/r).$$

The equilibrium exists provided $E < r$. Graphically, the equilibrium occurs at the intersection of the line En with the symmetric parabola $rn - (r/k)n^2$. The so-called sustainable yield curve is a plot of the equilibrium harvest rate, $E\hat{n} = kE - (k/r)E^2$ as a function of harvest effort, E. The Schaefer model has a symmetric sustainable yield curve, with the maximum sustainable yield (MSY) occurring at $E_{max} = r/2$ (see Clark [1976]).

Allee effects would considerably alter these predictions of the Schaefer model. Mating encounter limitation in the logistic has effects on the population similar to harvesting, as is true for the simple models without an upper equilibrium. Only, in the logistic model the effects are those of constant rate *plus* constant effort harvesting. Consider the model

$$(3.41) \qquad dn/dt = rn - (r/k)n^2 - E_1 - E_2 n,$$

where $E_1 = \theta(\lambda - \theta)$ and $E_2 = r\theta/k$. The equilibria of this model are exactly those of the encounter-limited logistic (3.30, 3.31). Additional harvesting by man effectively increases E_1 or E_2, exacerbating the consequences of the Allee effects.

The encounter-limited logistic (3.28) under constant effort harvesting becomes

$$(3.42) \qquad dn/dt = rn - (r/k)n^2 - \lambda\theta n/(\theta + n) - En.$$

Equilibria, $\hat{n}_1$ and $\hat{n}_2$, are given by the quadratic formulas (3.30) and (3.31), only with $A = -r/k$, $B = r(1 - \theta/k) - E$, and $C = \theta(r - \lambda - E)$. Harvesting increases the critical density, $\hat{n}_1$, and decreases the steady-state density, $\hat{n}_2$, as compared with the non-harvesting equilibria $\bar{n}_1$ and $\bar{n}_2$. The sustainable yield becomes $E\hat{n}_2$. A striking consequence of increasing the harvesting effort becomes clear from a graphical depiction of the harvesting rate superimposed on the population's biological growth rate (Figure 8). Population increase occurs when the difference of the growth rate and harvesting rate is positive. As E increases, $\hat{n}_1$ and $\hat{n}_2$ become closer and closer together, until merging upon reaching a harvest effort E^*. Setting $\hat{n}_1 = \hat{n}_2$, or $B^2 = 4AC$, and solving for E^*, we have

$$(3.43) \qquad E^* = r(1 + \theta/k) - 2\sqrt{\lambda\theta r/k}.$$

When $E > E^*$, the equilibria $\hat{n}_1$ and $\hat{n}_2$ vanish (become complex-valued), leaving 0 as the only system equilibrium. Such over-harvesting spells ultimate extinction for the population. The sustainable yield curve has an abrupt discontinuity at E^* (Figure 9). Clark [1976] presents a similar figure as a graphical model of "critical depensation." Harvesting such an encounter-limited population at MSY might be precariously close to exterminating the resource.
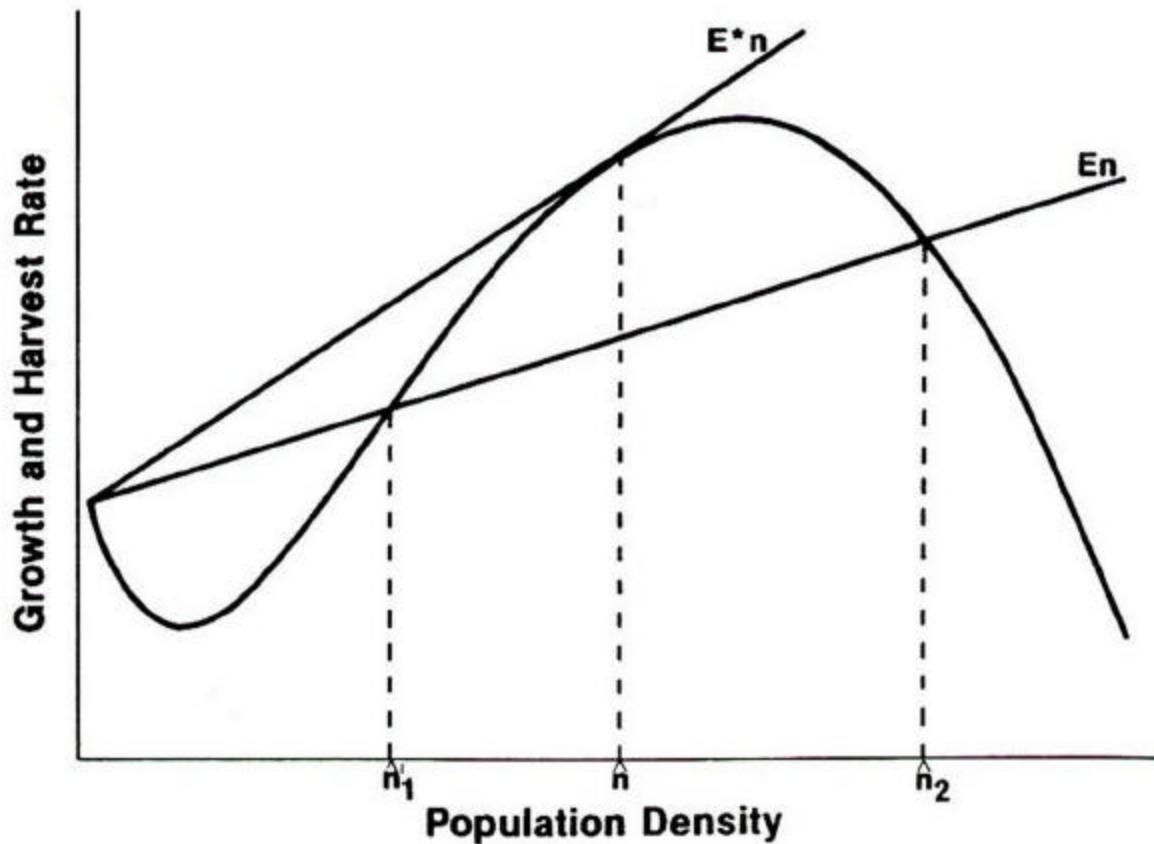
FIGURE 8. The RH-logistic harvesting model. Growth rate, $rn - (r/k)n^2 - \lambda\theta n/(\theta + n)$, and harvest rate, En, plotted as functions of n. Their intersections provide locations of equilibria, $\hat{n}_1$ and $\hat{n}_2$. Equilibria merge when $E = E^*$.

4. Stochastic growth. This section incorporates stochastic forces into the population growth models of §3. Those models served to quantify Allee's concept of a critical density within the framework of traditional deterministic modeling in ecology, and to establish the underlying dynamic behavior of populations experiencing Allee effects. The presence of stochastic forces, as will be seen in this section, considerably alters the deterministic predictions. For example, the deterministic models allow but one predicted population density to originate from a given initial density, m. Stochastic models afford a variety of possible outcomes from a given m value. A population below critical density might increase, and a population above critical density might decrease. The very concept of critical density, in fact, takes different forms in stochastic models.

The discrete birth-death processes discussed first in this section offer certain advantages as models of low density populations. The

FIGURE 9. The sustainable yield curve for the RH-logistic harvesting model.

assumption of §3 that n is a continuous variable applies more properly to larger populations (see May [1974, p. 30]). Discrete birth-death processes reflect the fact that organisms come in integer packages by treating population size as a discrete variable. Also, individual births and deaths in the population are modeled directly as stochastic events. Discrete pure birth models are constructed first in this section using the various encounter functions of §2. Attention centers on the stochastic counterpart to the waiting time defined for the deterministic birth models in §3. Later in this section, extinction probabilities are derived from various discrete birth-death models. If present, a critical density appears as an inflection point in the curve of extinction probability (or probability of never reaching a fixed large size before extinction) plotted as a function of m.

Continuous stochastic models, in the form of diffusion processes (or stochastic differential equations), are discussed at the end of this section. Such processes seem more appropriate for modeling populations

with an upper stable equilibrium, since discrete stochastic versions of models such as the logistic are awkward and artificial. Instead, continuous stochastic versions are simpler and portray more accurately the type of stochastic forces experienced by populations at high densities. This section shows that a critical density in continuous stochastic models appears as an inflection point in the probability of never reaching a fixed large population density before reaching a fixed small density. If a stationary probability distribution for population density exists, a critical density may be manifested as a local minimum in the distribution.

Discrete birth-death processes. The assumptions of discrete birth-death processes revolve around stochastic birth and death rates, $\lambda(n)$ and $\mu(n)$, respectively. The probability that a birth occurs in the population during a short time interval, Δt, is assumed to be

(4.1)
$$\Pr[N(t + \Delta t) = n + 1 \mid N(t) = n] = \lambda(n)\Delta t.$$

Population size, $N(t)$, is now a nonnegative, integer-valued random variable with a distribution that depends on t. The measurement units of $N(t)$ are numbers of organisms; dividing $N(t)$ by area produces population density at time t. Likewise the chance of a death during that interval is assumed to be

(4.2)
$$\Pr[N(t + \Delta t) = n - 1 \mid N(t) = n] = \mu(n)\Delta t.$$

The probability that two or more events occur in Δt is assumed negligible. Thus, neither a birth nor a death occurs during Δt with probability $1 - \lambda(n)\Delta t - \mu(n)\Delta t$. The rates $\lambda(n)$ and $\mu(n)$ are assumed homogeneous in time and space, and the population members are assumed homogeneous in their impacts on those rates. These assumptions specify a stochastic birth-death process. The probability distribution of $N(t)$ satisfies a system of "forward" differential equations and typically contains m and t as parameters (e.g., Bailey [1964], Feller [1968], Karlin and Taylor [1975]). Letting $\Pr[N(t) = n] = p_n(t)$, we have:

(4.3)
$$\frac{dp_n(t)}{dt} = \lambda(n-1)p_{n-1}(t) + \mu(n+1)p_{n+1}(t)$$
$$- [\lambda(n) + \mu(n)]p_n(t), \quad n = 0, 1, 2, \ldots .$$

Unfortunately, the distributions resulting from all but the simplest forms for $\lambda(n)$ and $\mu(n)$ are typically not available in closed form. Goel

and Richter-Dyn [1974] list most birth-death processes with known explicit distributions.

Clues about the dynamic behavior of these distributions become available by listing a few additional properties of birth-death processes (Karlin and Taylor [1975]): (1) the time, S_n, between events (an event being a birth or death) in a population of size n has an exponential distribution with $E[S_n] = 1/[\lambda(n) + \mu(n)]$; (2) the probability that the next event is a birth in a population of size n is $\lambda(n)/[\lambda(n) + \mu(n)]$; (3) the probability that the next event is a death is likewise $\mu(n)/[\lambda(n) + \mu(n)]$. Properties 1, 2, and 3 are, among other things, a recipe for simulating birth-death processes with computers.

The expected value of $N(t)$ by definition is some function of t:

$$(4.4) \qquad w(t) = E[N(t)] = \sum_{n=0}^{\infty} n p_n(t).$$

The function $w(t)$ satisfies a differential equation found by multiplying both sides of (4.3) by n and summing from $n = 0$ to ∞:

$$(4.5) \qquad dw/dt = \sum_{n=0}^{\infty} \lambda(n) p_n(t) - \sum_{n=0}^{\infty} \mu(n) p_n(t)$$
$$= E[\lambda(N(t))] - E[\mu(N(t))].$$

Since $E[\lambda(N(t))] = \lambda(w)$ if $\lambda(\cdot)$ is linear, equivalence of the deterministic model (3.1) to the mean of the stochastic model occurs when the birth and death rates are linear functions of n.

Pure birth processes. Stochastic pure birth processes set $\mu(n) = 0$ for all n. This assumption is reasonable if losses from the population are insignificant. Population decline or extinction, like the deterministic case, is not possible under a stochastic pure birth process. The encounter frequency models of §2 are birth processes: the "population" is the number of encounters, $X(a)$, and a plays the role of time. The complete probability density for $N(t)$ resulting from almost any arbitrary $\lambda(n)$ is available in closed form (Bartlett [1978, p. 58], see caption, Figure 10) or recursively (see equations (2.3) and (2.4)). Additionally, from property 1, the expected waiting time for the population to reach size n from initial size m is

$$(4.6) \qquad E[T] = E[S_m] + E[S_{m+1}] + \cdots + E[S_{n-1}] = \sum_{k=m}^{n-1} 1/\lambda(k),$$

where T is the waiting time (a continuous random variable). This expected waiting time in a sense may be compared to the waiting time (3.2) of the deterministic birth model. The stochastic mean waiting time (4.6) will always be greater than the deterministic waiting time (3.2) if $1/\lambda(n)$ is a decreasing function of n. The SL, BC, NE, and RH birth rates (Table 1) all have decreasing reciprocals, and thus yield longer stochastic waiting times.

(i) The birth process incorporating the SL birth rate was first introduced as a mathematical model of speciation (Yule [1924]). I here adopt the process in its more familiar context of population growth, to represent the null hypothesis of no Allee effects. The probability distribution for $N(t)$ is a shifted negative binomial (Figure 10). The expected value of $N(t)$, from (4.5), increases exponentially with time:

$$(4.7) \qquad E[N(t)] = me^{\lambda t}.$$

The equivalence of (4.7) to its deterministic counterpart (3.4) is a consequence of the fact that $\lambda(n)$ is linear in n.

The expected waiting time (4.6) is compactly expressed with a function, $\psi(\cdot)(= \Gamma'(\cdot)/\Gamma(\cdot))$, known as the digamma function:

$$(4.8) \qquad E[T] = \sum_{k=m}^{n-1} 1/(\lambda k) = (1/\lambda)[\psi(n) - \psi(m)].$$

This expression utilizes the fact that the digamma satisfies the recurrence relation $\psi(k+1) = \psi(k)+1/k$ (Abramowitz and Stegun [1965, p. 258]). A graph of $\psi(k)$ resembles, but is always less than, $\log k$. However, $\psi(k)$ increases faster than $\log k$ (approaching $\log k$ as $k \to \infty$). Also, (4.8) is greater than its deterministic counterpart (3.3) since $1/(\lambda n)$ is decreasing in n.

(ii) The expected waiting time for the BC birth process is (note that $\psi'(k+1) = \psi'(k) - 1/k^2$) :

$$(4.9) \qquad E[T] = \sum_{k=m}^{n-1} 1/(\lambda \alpha k^2) = [1/(\lambda \alpha)][\psi'(m) - \psi'(n)].$$

Noting also that $d \log n/dn = 1/n$, we see that (4.9) bears the same relationship to (4.8) as does (3.5) to (3.3). Also, (4.9) is greater than (3.5).

This birth process additionally displays a stochastic equivalent of the explosive growth seen in the deterministic model. Since $\psi'(n) \to 0$ as $n \to \infty$, $E[T] \to \psi'(m)/(\lambda\alpha)$, implying that the expected waiting time until the system becomes infinite is finite. The transition probabilities for $N(t)$ are deficient (sum to less than one): there is positive probability that the population becomes infinite in a finite time t (Feller [1968, p. 451]). Clearly, this process offers at best an approximation of very low populations for brief intervals only.

(iii), (iv) The RH or NE birth processes are not explosive. The probabilities for $N(t)$ always sum to one and always lag behind those of the SL process (Figure 10). This property would seem more representative of a population experiencing an Allee effect. The RH version again proves more tractable than the NE version. For instance, the expected RH waiting time contains "contributions" from an SL birth process and a BC birth process:

$$(4.10) \quad E[T] = \sum_{k=m}^{n-1} 1/(\lambda k) + \sum_{k=m}^{n-1} \theta/(\lambda k^2) = (1/\lambda)[\psi(n) - \psi(m)]$$

$$+ (\theta/\lambda)[\psi'(m) - \psi'(n)].$$

Thus, $E[T]$ under the RH birth process is increased over that of the SL process (4.8) by an amount proportional to the expected waiting time of a BC process (4.9). The proportionality constant is again θ (recalling (3.7), (3.5), and (3.3)). However, (4.10) is always greater than (3.7) for the same values of λ, θ, m, and n, since $1/\lambda(n) = (n + \theta)/(\lambda n^2)$ is decreasing in n. Similar expressions for the NE process are available but are quite messy (Dennis [1982]).
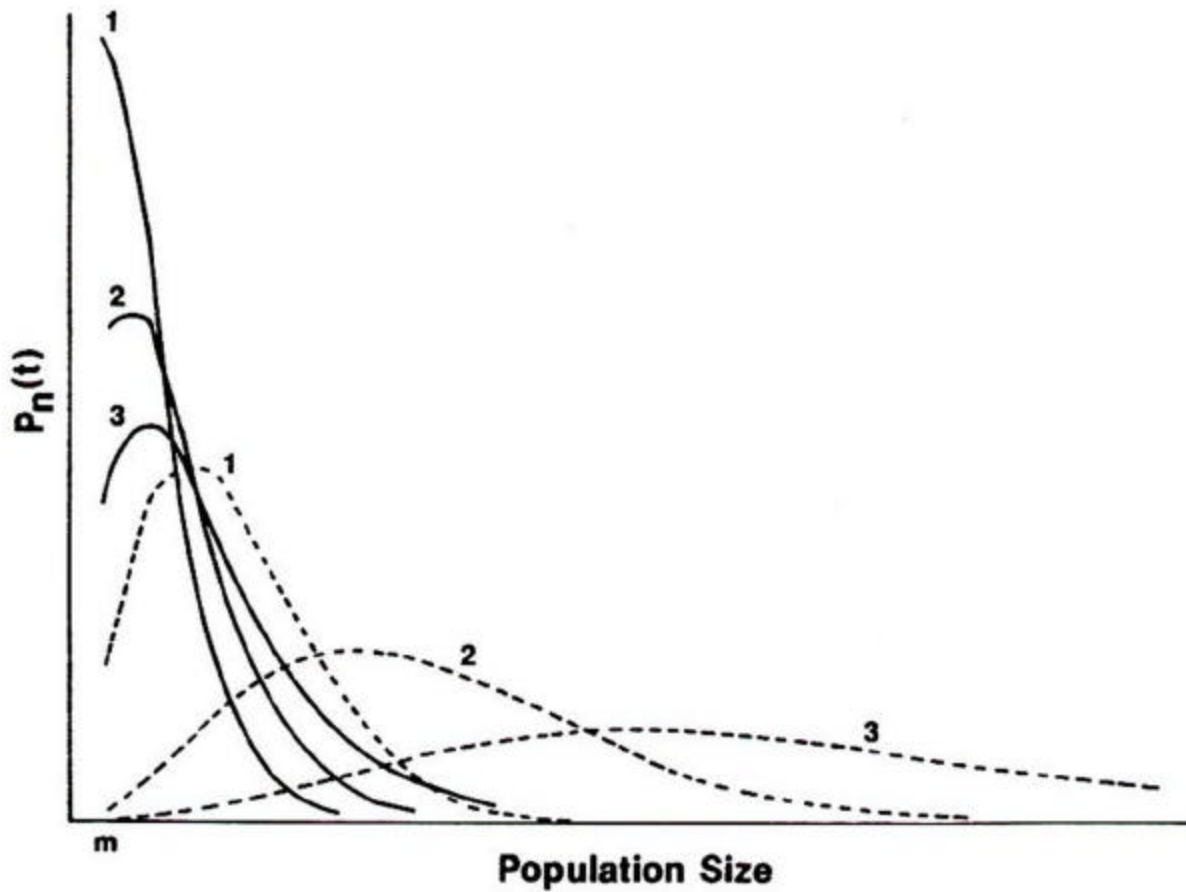
FIGURE 10. Dashed lines show the probability distribution of $N(t)$ for various values of t under the SL birth process. The pdf is

$$p_n(t) = \binom{n-1}{m-1} e^{-\lambda t m} (1 - e^{-\lambda t})^{n-m}, n = m, m+1, \cdots.$$

Solid lines depict the distribution for the NE birth process. The pdf is

$$p_n(t) = (-1)^{n-m} \prod_{i=m}^{n-1} \lambda(i) \sum_{j=m}^{n} \left\{ e^{-\lambda(j)t} \bigg/ \prod_{\substack{k=m \\ k \neq j}}^{n} (\lambda(j) - \lambda(k)) \right\}, \quad n = m, m+1, \ldots,$$

where $\lambda(n) = \lambda n (1 - e^{-\beta n})$.

Birth-death processes. Models allowing the possibilities of decline and extinction are appropriate when mortality losses are significant. Population size in stochastic birth-death processes undergoes a random walk on the non-negative integers with the time between jumps varying according to property 1 discussed earlier. I will assume mortality takes the form $\mu(n) = \mu n$. Of particular interest is the probability, denoted $\xi(m)$, that the population goes extinct from an initial size m. Properties 2 and 3, discussed earlier, define a recursion relation for $\xi(m)$:

$$
\begin{aligned}
\xi(m) = {} & \xi(m+1)\lambda(m)/[\lambda(m)+\mu(m)] \\
& + \xi(m-1)\mu(m)/[\lambda(m)+\mu(m)].
\end{aligned}
$$

(4.11)

This relation merely decomposes "extinction from size m" into two mutually exclusive events: (1) a birth occurs, followed by extinction from size $m+1$, and (2) a death occurs, followed by extinction from size $m-1$. The solution to (4.11) is readily found to be (e.g., Karlin and Taylor [1975, p. 145]).

$$
\xi(m) = \sum_{x=m}^{\infty} v(x) \Big/ \sum_{x=0}^{\infty} v(x),
$$

(4.12)

where

$$
v(x) = \begin{cases} 1, & x = 0, \\ \dfrac{\mu(1)\mu(2)\cdots\mu(x)}{\lambda(1)\lambda(2)\cdots\lambda(x)}, & x = 1, 2, \ldots, \end{cases}
$$

(4.13)

under the condition that $\Sigma v(x)$ converges. Extinction is certain if the sum does not converge. In practice, the form of $\xi(m)$ is quite generally the summed right tail probabilities of a discrete probability distribution (Dennis [1981]):

$$
\xi(m) = \sum_{x=m}^{\infty} p(x).
$$

(4.14)

Here $p(x)$ is a discrete probability mass function defined on the non-negative integers with the recurrence relationship

$$
p(x)/p(x-1) = \mu(x)/\lambda(x).
$$

(4.15)

Note that a mode of $p(x)$ corresponds to an inflection point in $\xi(m)$ plotted as a function of m. A mode $\bar{m}$ is defined here as a value of x where $p(\bar{m} - 1) < p(\bar{m}) > p(\bar{m} + 1)$. Since $\xi(m) - \xi(m + 1) = p(m), m = 0, 1, \ldots$, one finds that $\xi(\bar{m}-1)-\xi(\bar{m}) < \xi(\bar{m})-\xi(\bar{m}+1) > \xi(\bar{m} + 1) - \xi(\bar{m} + 2)$ if $\bar{m}$ is a mode of $p(x)$. Furthermore, a mode of $p(x)$, and the resulting inflection point in $\xi(m)$, corresponds to a deterministic unstable equilibrium. An unstable equilibrium $\bar{n}$ is given by $\lambda(\bar{n}) = \mu(\bar{n})$, where $\mu(n) > \lambda(n)$ for $n < \bar{n}$ and $\mu(n) < \lambda(n)$ for $n > \bar{n}$, in a local region of n values containing $\bar{n}$. The recursion relationship (4.15) implies that $\mu(\bar{m})/\lambda(\bar{m}) > 1$ and $\mu(\bar{m} + 1)/\lambda(\bar{m} + 1) < 1$ when $\bar{m}$ is a mode of $p(x)$; thus $\bar{m} < \bar{n} < \bar{m} + 1$.

(i) Ecologists have used the SL birth-death process as a stochastic model of a species colonizing an island (MacArthur and Wilson [1967], MacArthur [1972, p. 121], Crowell [1973]). The full probability distribution for $N(t)$ is available in closed form but is somewhat lengthy (e.g., Bailey [1964, p. 94], see also Richter-Dyn and Goel [1972], for many additional properties of this model). The probability of extinction is, from (4.14) and (4.15), the right tail of a geometric probability distribution (provided $\lambda > \mu$):

$$(4.16) \qquad \xi(m) = \sum_{x=m}^{\infty} [1 - (\mu/\lambda)](\mu/\lambda)^x = (\mu/\lambda)^m.$$

A plot of $\xi(m)$ as a function of m declines in the characteristic geometric fashion (Figure 11).

(ii) The BC birth-death process is explosive; an infinite number of births can occur in finite time. However, the process admits a possibility of extinction due to the positive death rate. The chance of that event is the tail of a Poisson distribution:

$$(4.17) \qquad \xi(m) = \sum_{x=m}^{\infty} e^{-\mu/(\lambda\alpha)}[\mu/(\lambda\alpha)]^x/x! = \gamma(m, \mu/(\lambda\alpha))\Gamma(m).$$

Here $\gamma(\cdot, \cdot)$ is the incomplete gamma function (Gradshteyn and Ryzhik [1965, p. 940]). If $\lambda\alpha > \mu$, (4.17) as a function of m resembles (4.16) in shape. If $\lambda\alpha < \mu$, $\xi(m)$ acquires a declining sigmoid shape: the extinction probabilities remain high until abruptly decreasing within a small range of m values. The inflection point of $\xi(m)$, $\bar{m}$ say,
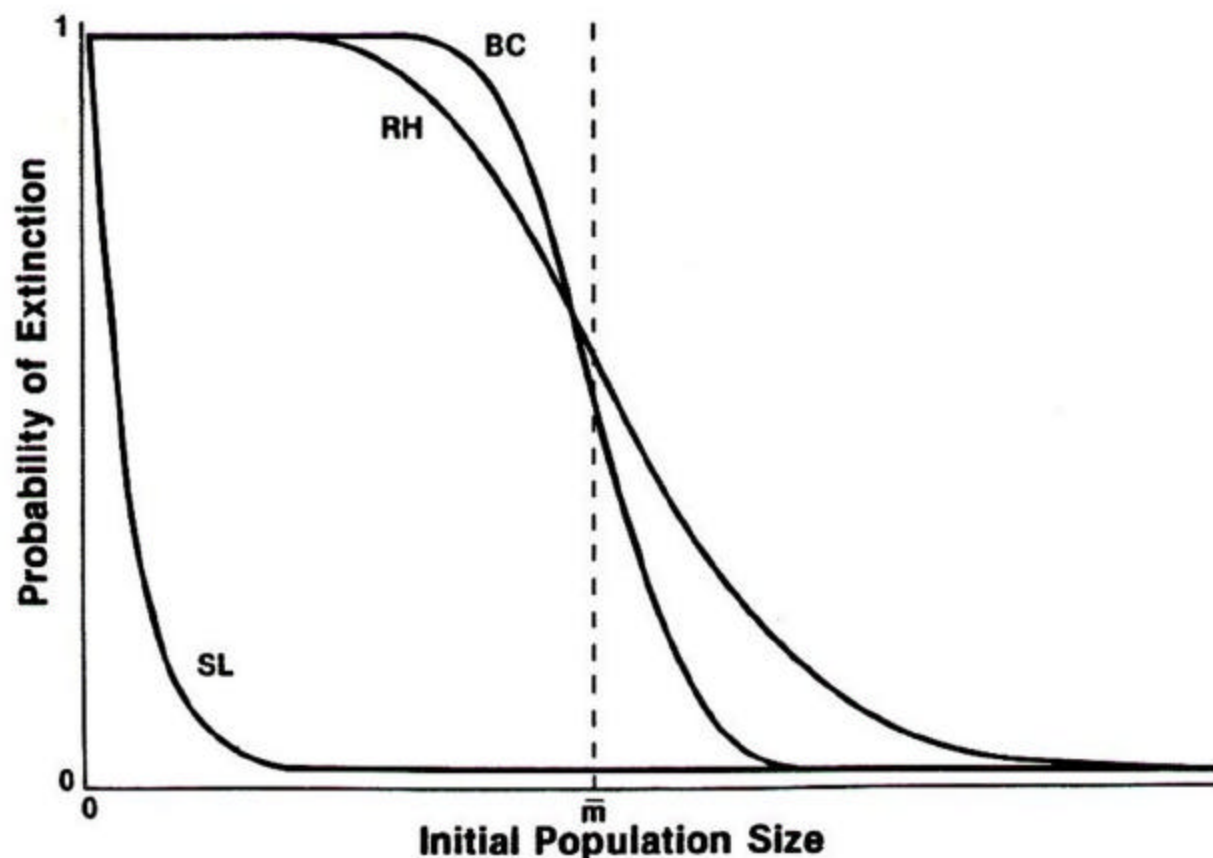
FIGURE 11. The probability of extinction, $\xi(m)$, plotted as a function of
initial population size m. Shown are the SL model (4.16), the BC model
(4.17), and the RH model (4.18).

occurs at $\bar{m} \approx \mu/(\lambda\alpha)$. This quantity corresponds to the mode of
the Poisson probabilities in (4.17); it also is the population size near
which $\lambda(n) = \mu(n)$. Thus, the critical size $\bar{m}$ is the counterpart to the
deterministic critical density of (3.12). These properties of $\xi(m)$ in the
BC model foreshadow similar properties in the RH and NE versions.

Interestingly, a population harvesting model leads to the same chance
of extinction as does the BC model. Envision a population with an SL
birth rate that is harvested at a constant (stochastic) rate μ/α. In
other words, $\lambda(n) = \lambda n$ and $\mu(n) = \mu/\alpha$. The probability of extinction
for this process is exactly (4.17). This parallel between encounter
limitation and harvesting also emerges in the subsequent models.

(iii), (iv) Birth-death processes utilizing the NE and RH birth rates
have similar dynamic behavior. The probabilities for $N(t)$ tend to pile
up at low values of n when m is less than the critical size, and they
disperse, slowly at first, toward higher values of n when m is greater

than the critical size.

The probability of extinction for the RH model is, from (4.14) and (4.15), the right tail of a negative binomial distribution:

$$(4.18) \qquad \xi(m) = \sum_{x=m}^{\infty} \binom{\theta + x}{x} [1 - (\mu/\lambda)]^{\theta+1} (\mu/\lambda)^x.$$

This function of m displays the declining sigmoid shape for values of $\theta > (\lambda - \mu)/\mu$ (Figure 11). The curve shows extinction probabilities for small populations greatly increased over those of the SL model (4.16) when θ represents a sizeable fraction of m. The RH extinction probability is greater than (4.16) for all m if $\theta > 0$; by contrast the BC extinction probability is much smaller than (4.16) for high m values due to the absurdly high birth rate. The inflection point of $\xi(m)$ again occurs approximately at the critical size: $\bar{m} \approx \theta\mu/(\lambda-\mu)$. The quantity $\bar{m}$ also corresponds to the mode of the negative binomial distribution in (4.18). Setting $\theta = 0$ in the RH birth rate of course recovers the SL birth rate. Note that the geometric distribution (4.16) is a special case of (4.18). Additionally, (4.18) is equivalent to the left tail of a binomial distribution under the circumstance that θ is an integer (Patil [1960]):

$$(4.19) \qquad \xi(m) = \sum_{x=0}^{\theta} \binom{m + \theta}{x} [1 - (\mu/\lambda)]^x (\mu/\lambda)^{m+\theta-x}.$$

A harvesting model yields an identical extinction probability. Consider a population growing according to the SL birth-death process that is harvested at a constant rate, $\mu\theta$. Thus $\lambda(n) = \lambda n$, and $\mu(n) = \mu n + \mu\theta$. The probability of extinction is exactly (4.18). The parallel between encounter limitation and harvesting makes intuitive sense: failure to find fellow species members essentially removes organisms from the reproductive process. As seen in §3, a similarity between Allee effects and harvesting manifests itself in the equilibria of the deterministic models.

Many stochastic processes proposed in the conservation biology literature as rare species models predict certain extinction (e.g. Goodman [1987]). Such models typically have an upper reflecting boundary, representing a maximum population size that a region can support. The studies focus upon properties of the mean time to extinction instead of

the probability of extinction. I chose not to emphasize such models in this paper, because: (a) an upper reflecting boundary is a difficult parameter to estimate from data sets (see Dennis [1989] for approaches to estimating parameters in stochastic population models); (b) unbounded processes offer reasonable approximations to the stochastic properties of bounded processes at low population sizes; (c) diffusion processes, discussed later in this section, provide in my judgement more realistic descriptions of population fluctuations at high densities. Nonetheless, I sketch here a feature of Allee effects in birth-death models with or without a maximum population size.

For birth-death processes with an absorbing state at zero, a critical size corresponds to an inflection point in the probability of never attaining a large population size n from an initial size m (where n is larger than the deterministic critical equilibrium $\bar{n}$). Let $\xi(m; n)$ denote the probability of never attaining n from m (i.e., of extinction before reaching size n). Goel and Richter-Dyn ([1974, p. 20]) listed a formula for $\xi(m; n)$ in terms of the stochastic birth and death rates. The formula can be expressed as

$$(4.20) \qquad \xi(m; n) = \sum_{x=m}^{n-1} v(x) \Big/ \sum_{x=0}^{n-1} v(x),$$

where $v(x)$ is defined by (4.13). This expression holds regardless of whether or not an upper reflecting boundary exists. Notice this is the right tail of a discrete probability distribution defined on the integers $0, 1, 2, \ldots, n-1$. The recursion relationship for the probability distribution is

$$(4.21) \quad [\xi(x; n) - \xi(x+1; n)] \, / \, [\xi(x-1; n) - \xi(x; n)] = \mu(x)/\lambda(x),$$

identical to the recursion relationship (4.15) for $p(x)$ in the probability of extinction. By an argument identical to that for $\xi(m)$ (below (4.15)), $\xi(m; n)$ plotted as a function of m has an inflection point near an unstable equilibrium $\bar{n}$.

If extinction is not certain, the infinite sum $v(0) + v(1) + v(2) + \ldots$ converges, and $\xi(m) = \xi(m; \infty)$. The probability of never reaching n before extinction (4.20) can then be written as

$$(4.22) \qquad \xi(m; n) = \sum_{x=m}^{n-1} p(x) \, \Big/ \, \sum_{x=0}^{n-1} p(x),$$

where $p(x)$ is the probability distribution associated with $\xi(m)$ (4.14). Here, $\xi(m; n)$ becomes the right tail of a truncated version of the probability distribution defined by $p(x)$.

Extinction data. Data on extinction probability as a function of population size are scarce. Mason [1977] presents evidence of density dependent extinction in ambushbugs, but specific quantitative relationships are not discernable. Crowell [1973] experimentally introduced different densities of small rodent species (*Peromyscus* sp. and *Clethrionomys* sp.) onto islands in the Gulf of Maine, and he collected data on the resulting populations through many years of field work. He noted that the data were generally consistent, to an order of magnitude, with the SL stochastic birth-death model (the parameters λ and μ were estimated from natality and mortality data, not from extinction data). Interestingly, Crowell's observed extinction frequencies for *Peromyscus* show a hint of sigmoid shape when plotted as a function of initial population size (Figure 12). The *Clethrionomys* data appear not to have an inflection point. However, not enough data exist in either case to justify applying an asymptotic statistical test, derived by Dennis [1982], of the SL vs. the RH extinction curves.

Laboratory experiments to obtain data for such a test would be feasible for numerous organisms. Normally, the probability of mates not finding each other in a laboratory culture vessel would be extremely low, unless the culture vessel were so large as to be unwieldy to sample or maintain. The parameter θ, if positive, would be too small to detect with extinction experiments under usual laboratory conditions. The key to detecting whether θ is positive is to increase the death rate by artificially removing organisms. Prolific laboratory invertebrates can repopulate a culture after only one mating: λ is usually high compared to μ. If μ is increased artificially, though, the effect is to amplify the sigmoid shape of the extinction curve (4.18) through increasing the critical size $\bar{m}$. If θ is not positive, the extinction curve would maintain the SL geometric shape (4.16) even under an artificially high death rate.

Continuous diffusion processes. Discrete, birth-death stochastic versions of the logistic model do not seem entirely satisfactory. The problem, if I may call it that, is a certain vagueness about the birth and death rates in the logistic. Any forms for $\lambda(n)$ and $\mu(n)$ will do, so long as $\lambda(n)/n - \mu(n)/n$ is a linear declining function of n.
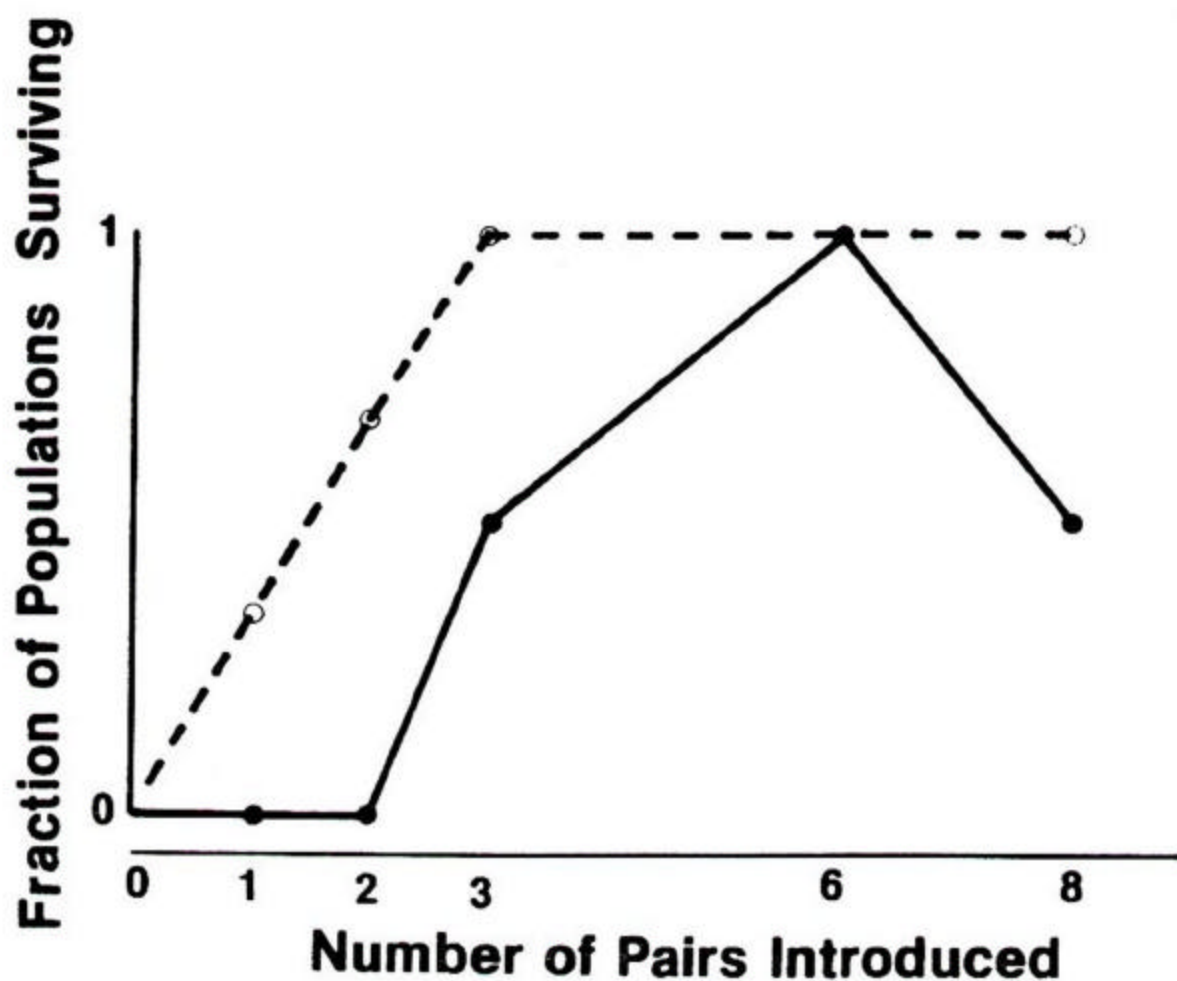
FIGURE 12.   Proportion of colonizing populations surviving (= 1−
probability of extinction) plotted as a function of initial population size.
Open circles: *Clethrionomys* sp.   Solid circles: *Peromyscus* sp.   Data are
from Crowell [1973].

Birth-death processes commit the model builder to more specific as-
sumptions concerning $\lambda(n)$ and $\mu(n)$. One might assume, for instance,
that $\lambda(n) = (a - bn)n$ for $n < a/b$, $\lambda(n) = 0$ for $n \geq a/b$, and
$\mu(n) = (c + dn)n$ (Pielou [1977, p. 27]). However, this eliminates
any chance of birth occurring for $n \geq a/b$ and hence any chance of the
population drifting stochastically above a/b. The effect is an artificial,
rigid barrier at a/b that bounces the population downward. Such re-
flecting boundaries in population models have the additional drawback
of being nearly inestimable (in the statistical sense) from data.

As noted in §3, the logistic is an approximation to continuous popu-
lation models of the form listed in equations (3.20), (3.21), and (3.22).
Such a general form does not necessarily specify birth and death rates,

but only specifies a net population growth rate, $ng(n)$. Here I discuss a stochastic version of (3.20) that preserves this character of the underlying deterministic model. Also, the equilibrium population sizes are likely to be quite large. Using discrete processes to model population fluctuations around a large steady state introduces unnecessary mathematical complications, while the continuous models at large population sizes offer good approximations and are much simpler.

A stochastic treatment maintaining the spirit of deterministic models of the form (3.20) is to introduce "white noise" into the per-individual growth rate, $g(n)$:

$$(4.23) \qquad dN(t) = N(t)g(N(t))dt + \sigma N(t)dZ(t),$$

where $Z(t)$ is a standard Wiener (Brownian motion) process, and σ is a positive parameter. In this model, $N(t)$ is a continuous stochastic process known as a diffusion process. The noise phenomenologically represents effects of unpredictable environmental fluctuations on the per-individual growth rate. Such stochastic forces are commonly termed "environmental," as opposed to the "demographic" stochastic forces of the discrete birth-death processes treated earlier (May [1974]). The fluctuations in the population growth rate given by the expression $\sigma N(t)dZ(t)$ are termed "multiplicative noise" and lead to many types of emergent system behavior (e.g. Dennis and Costantino [1988]). Lucid accounts of the mathematical details involved in such stochastic differential equations are available (Goel and Richter-Dyn [1974], Ludwig [1974], Ricciardi [1977], Karlin and Taylor [1981]). Many probabilistic properties for this type of model, such as transition probability distributions and waiting time distributions, have been derived, Goel and Richter-Dyn [1974] catalogued many known results (see also Haken [1983a, b], Risken [1983], Horsthemke and Lefever [1984]).

I restrict attention here to two properties: (a) the probability of never attaining an upper population density before attaining a low one (analogous to $\xi(m, n)$ in discrete birth-death processes (4.20)), and (b) the stationary probability distribution for population density. A critical density caused by Allee effects manifests itself in both quantities.

A critical density appears as an inflection point in the probability of reaching a small population density before reaching a large one. Let $\xi(m, x, n)$ denote the probability of never reaching population

density n from initial density m before attaining a low density x, where $0 < x \le m \le n$. The density x could represent a low point where extinction is certain (perhaps $x = 1$). A result listed by Goel and Richter-Dyn [1974, p. 62] applied to the particular stochastic differential equation (4.23) yields

$$(4.24) \qquad \xi(m; x, n) = \int_m^n \exp[-\phi(y)]\, dy \Big/ \int_x^n \exp[-\phi(y)]\, dy,$$

where

$$(4.25) \qquad \phi(y) = (2/\sigma^2) \int [g(y)/y]\, dy + 2[1 - (\omega/\sigma^2)] \log y.$$

Here ω is an indicator constant reflecting whether an "Ito" or a "Stratonovich" stochastic integral is used for interpreting the stochastic differential equation (4.23) (Ito: $\omega = \sigma^2$; Stratonovich: $\omega = \sigma^2/2$). The technical distinctions between the two types of stochastic calculi are unimportant for the results in this paper (see Mortensen [1969], Ricciardi [1977], Braumann [1983] for information about the distinctions). Interestingly, $\xi(m; x, n)$ is the right tail of a continuous probability distribution defined on the real interval (x, n), which parallels the result (4.20) for $\xi(m; n)$ in discrete birth-death processes.

If present, an inflection point in $\xi(m; x, n)$ plotted as a function of m (with x and n fixed) is a root of $\partial[-\log(\partial\xi/\partial m)]/\partial m = 0$. One easily finds from (4.24) that an inflection point, $\bar{m}$, is a solution of

$$(4.26) \qquad g(\bar{m}) + (\sigma^2 - \omega) = 0.$$

Recall that deterministic stable or unstable equilibria are roots of $g(\bar{n}) = 0$. Thus, inflection points of $\xi(m; x, n)$ correspond exactly to underlying deterministic equilibria when the stochastic differential equation (4.23) is interpreted in the Ito sense (and approximately in the Stratonovich sense). In particular, a lower critical density marks a point of locally steepest decline in the function $\xi(m; x, n)$. By contrast, an upper stable equilibrium is indicated by a point of locally most gentle decline in $\xi(m; x, n)$.

A critical density can also become evident in the stationary probability distribution for population density, if such a distribution exists.

The transition probability distribution for $N(t)$ in (4.23) changes with time; in some models, the transition distribution approaches a stationary distribution as time gets large:

$$(4.27) \qquad f(n) = K \exp\{(2/\sigma^2) \int [g(n)/n] \, dn - (2\omega/\sigma^2) \log n\},$$

$$0 < n < \infty.$$

Here $f(n)$ is the probability density function for the stationary distribution. The quantity K is a normalization constant found by setting the area under the curve $f(n)$ equal to one. Dennis and Patil [1984] discussed the role of this distribution in population ecology and its relationship to underlying deterministic stable or unstable equilibria. They also showed that the *form* of the stationary distribution (e.g. lognormal, gamma, etc.) is invariant under either the Ito or Stratonovich calculus.

The function $f(n)$ portrays the long-run stochastic history of population size fluctuating around a steady state. If $g(n)$ is approximated by a straight line (see (3.23)), the underlying deterministic model is the logistic equation. Substituting $g(n) = r - (r/k)n$ into (4.23) produces a stochastic logistic model (see Dennis [1989] for various properties of this model). In particular, the stationary distribution (4.27) for this stochastic logistic is a gamma distribution of population density:

$$(4.28) \qquad f(n) = K n^{s-1} e^{-an}, \quad 0 < n < \infty,$$

where $a = 2r/(k\sigma^2)$, $s = (2r/\sigma^2) + 1 - (2\omega/\sigma^2)$, and $K = a^s/\Gamma(s)$. The mode, or region of the most likely population size, is smaller than the mean population size (Figure 13).

The gamma distribution has been shown to give an extremely accurate portrayal of laboratory flour beetle populations fluctuating around a steady state (Dennis and Costantino [1988]).

Stochastic logistic-type models with mating encounter limitation can be similarly constructed. The version using the RH mating function is, from (3.28) and (4.23),

$$(4.29) \quad dN(t) = N(t)[r - (r/k)N(t) - \lambda\theta/(\theta + N(t))]dt + \sigma N(t)dZ(t).$$
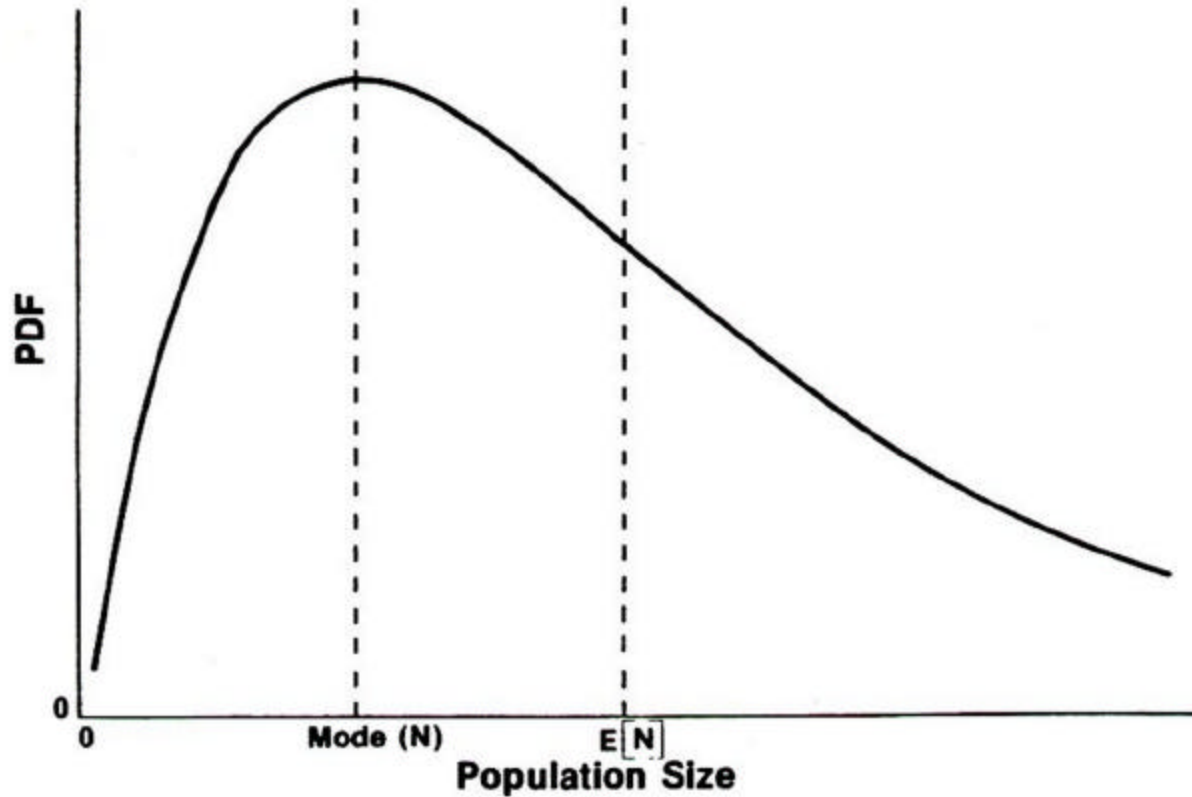
FIGURE 13. The gamma distribution of population abundance. The expected population size, E[N], is greater than the most likely population size (mode).

The stationary distribution resulting from (4.29) and (4.27) is a type of weighted gamma distribution:

$$(4.30) \qquad f(n) = Kn^{s-\gamma-1}e^{-an}(\theta+n)^{\gamma}, \quad 0 < n < \infty.$$

Here $\gamma = 2\lambda/\sigma^2$, and a and s are given with equation (4.28). The normalization constant K is complicated and is given by Dennis and Patil [1984]. A typical shape of (4.30) has several interesting features (Figure 14): (1) $f(n) \to \infty$ as $n \to 0$. (2) $f(n) \to 0$ as $n \to \infty$. (3) A local *minimum* (antimode), $\tilde{n}_1$ say, exists at

$$(4.31) \qquad \tilde{n}_1 = [-B + (B^2 - 4AC)^{1/2}]/(2A).$$

where $A = -r/k$, $B = r(1 - \theta/k) - \omega$, and $C = \theta(r - \lambda - \omega)$. (4) A local *maximum* (mode), $\tilde{n}_2$, exists at

$$(4.32) \qquad \tilde{n}_2 = [-B - (B^2 - 4AC)^{1/2}]/(2A).$$

Interestingly, (4.31) and (4.32) are exactly identical to the deterministic *harvesting* equilibria of (3.42), with the constant ω in the role of the harvesting effort, E. Consequently, (4.31) is larger than the non-harvesting deterministic critical density (3.30), while (4.32) is smaller than the non-harvesting deterministic steady state (3.31). In a sense, an antimode, or unlikely region of population size, is a stochastic manifestation of a deterministic critical density. Multiplicative noise magnifies the effects of mating limitation, though, by increasing the size of the antimode over that of the deterministic critical density. For high noise levels (high σ^2), the stationary distribution (4.30) ceases to exist (i.e., is not integrable at zero), and the population faces certain extinction, even if the initial population size is above the deterministic critical density (Dennis and Patil [1984]). This is an example of a "noise-induced transition," a type of emergent dynamic behavior common in stochastic systems (Horsthemke and Lefever [1984]).

Continuous stochastic models constructed from the BC-logistic (3.24) and the NE-logistic (see discussion of (3.28)) have properties similar to the RH version. The resulting stationary probability densities are, respectively,

(4.33) (BC) $f(n) = Kn^{s-1}\exp[an - bn^2], \quad 0 < n < \infty;$

(4.34) (NE) $f(n) = Kn^{s-1}\exp[-an - b\mathrm{Ei}(-\beta n)], \quad 0 < n < \infty.$

The constants in the above distributions are: (BC) $s = -(2\mu/\sigma^2) - (2\omega/\sigma^2) + 1, a = 2\lambda\alpha/\sigma^2, b = \gamma/\sigma^2;$ (NE) $s = (2r/\sigma^2) - (2\omega/\sigma^2) + 1, a = 2r/(k\sigma^2), b = 2\lambda/\sigma^2.$ The normalization constants are best left to a computer.

5. Conclusions. In this paper I have proposed some quantitative theories for addressing Allee's question about the minimal numbers necessary for a species' survival. Few data are available on this question; in fact, Andrewartha and Birch's [1954, p. 335]) appraisal of the topic is still true thirty-five years later: "This is at present, one of the most important and most neglected branches of population ecology." Large amounts of data, however, would shed little light on the question without a framework of mathematical models for hypothesis testing and interpretation. The models presented here
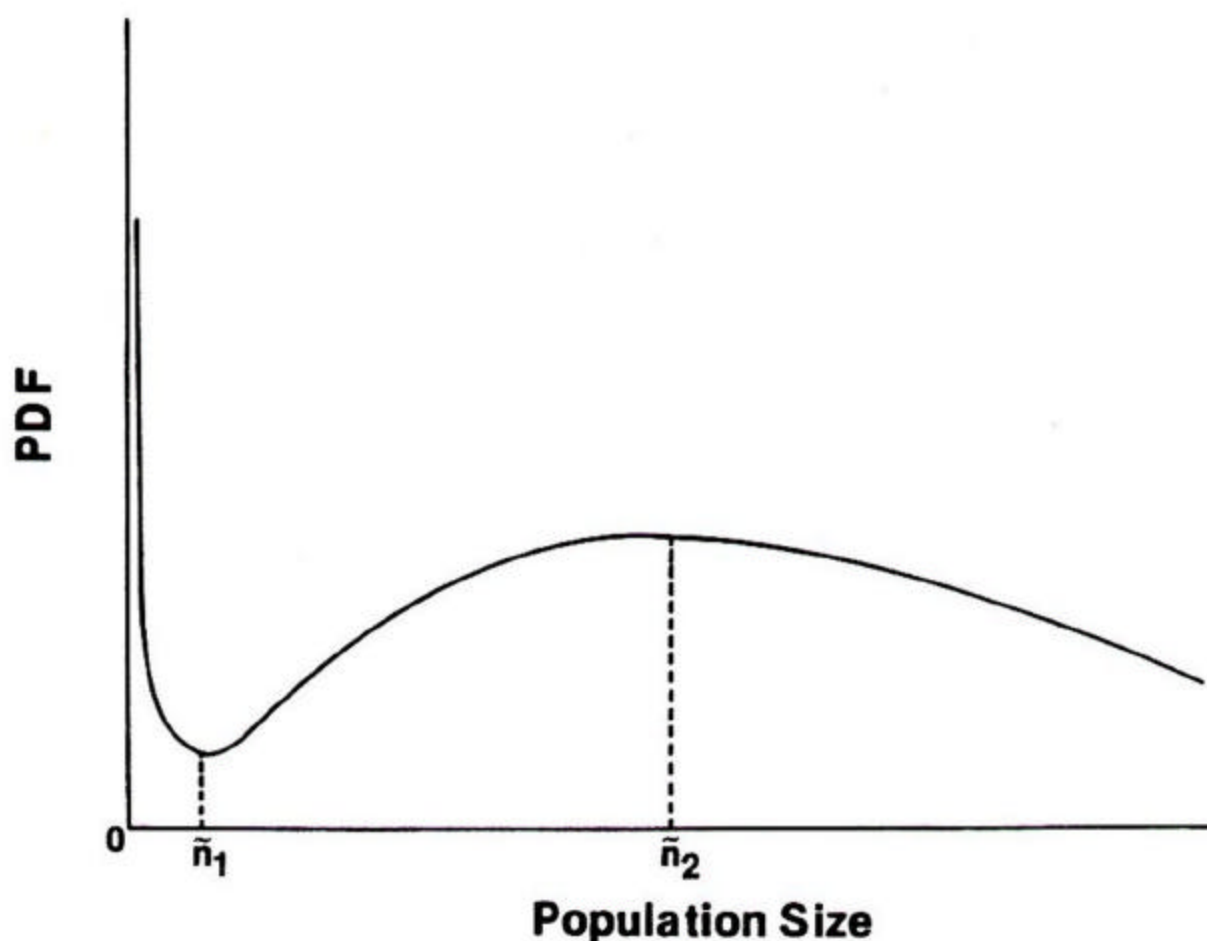
FIGURE 14. A typical shape of the stationary distribution (4.30) for the stochastic RH-logistic model. The antimode, $\tilde{n}_1$, is a stochastic equivalent of a critical density.

are relatively simple; I considered it important to concentrate on building a foundation of basic biological concepts before more detailed bioeconomic superstructures are erected.

A species' critical density is manifested differently in different types of population models. The basic concept of a critical density is a point where the net per-individual growth rate is zero but increasing as a function of population density. In a traditional deterministic differential equation model, a critical density is simply an unstable equilibrium, below which a population is doomed to extinction, above which a population survives. In a stochastic discrete birth-death process, though, a critical size appears as a sudden drop in the probability of extinction plotted as a function of initial population size. In a stochastic continuous diffusion process, a critical density corresponds to an unlikely region of population density. It also corresponds to a sudden drop

in the probability of reaching a small population density (extinction) before a large one, plotted as a function of initial density.

Allee effects would seriously impact management of biological resources. Populations experiencing Allee effects have dynamic properties similar to harvested populations, since organisms that fail to encounter fellow species members are effectively removed from the reproducing population. Actual harvesting would therefore amplify existing Allee effects by increasing the critical density. Some types of stochastic forces, multiplicative noise in particular, also exacerbate Allee effects. Recent theories of managing biological reserves for species preservation are based on stochastic population models lacking Allee effects. These models give overly optimistic predictions if the target species do indeed have Allee effects. Sparse, encounter-limited populations might fail to respond to management efforts aimed at habitat or carrying capacity improvement. An Allee effect unfortunately would be very difficult to detect or measure in a natural population.

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