

# **Allee effects in stochastic populations**

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“... what minimal numbers are necessary if a species is to maintain itself in nature?” (Allee 1938, *The Social Life of Animals*)

“This is, at present, one of the most important and most neglected branches of population ecology.”  
(Andrewartha and Birch 1954, *The Distribution and Abundance of Animals*, commenting on the reduction of  $r$  in sparse natural populations)

Allee effect: situation in which the per-unit-abundance growth rate of a population is an increasing function of abundance

after W. C. Allee (1931, *Animal Aggregations*, 1938  
*The Social Life of Animals*)

(inverse density dependence, depensation)

biological mechanisms:

rare matings

social facilitation of  
reproduction

cooperative hunting

social protection from predation

reviews:

Kramer et al. 2009 The evidence for Allee effects. *Population Ecology*, in press.

Courchamp et al. 2008 *Allee Effects in Ecology and Conservation*, Oxford Univ. Press.

*TREE*, October 1999, vol  
14(10)

Dennis 1989 Allee effects: population growth, critical density, and the chance of extinction *Natural Resource Modeling* 3:481-538

models:

primarily *deterministic*

date to Volterra (!) 1938 *Human  
Biology* 3:1-11.

goals of this presentation:

develop stochastic aspects

examine “critical density”

concept

predict patterns likely to be

observed in data when

Allee effects are present

# deterministic models

$$\frac{dn}{dt} = m(n)$$

where  $n$  is population abundance at time  $t$ , and  $m(n)$  is a function specifying any density dependence

An equilibrium  $\tilde{n}$  is a root of

$$m(\tilde{n}) = 0$$

*ex.* no Allee effect

$$\frac{dn}{dt} = \lambda n - \mu n$$

(exponential increase/decrease)

$$\frac{dn}{dt} = r n - \frac{r}{k} n^2$$

(logistic,  $\tilde{n} = k$ )



*ex.* Allee effect

$\frac{n}{\theta + n}$  model of frequency or probability of contact, per individual, in population of size  $n$  (Dennis 1989)

$$\frac{dn}{dt} = \lambda n \frac{n}{\theta + n} - \mu n$$

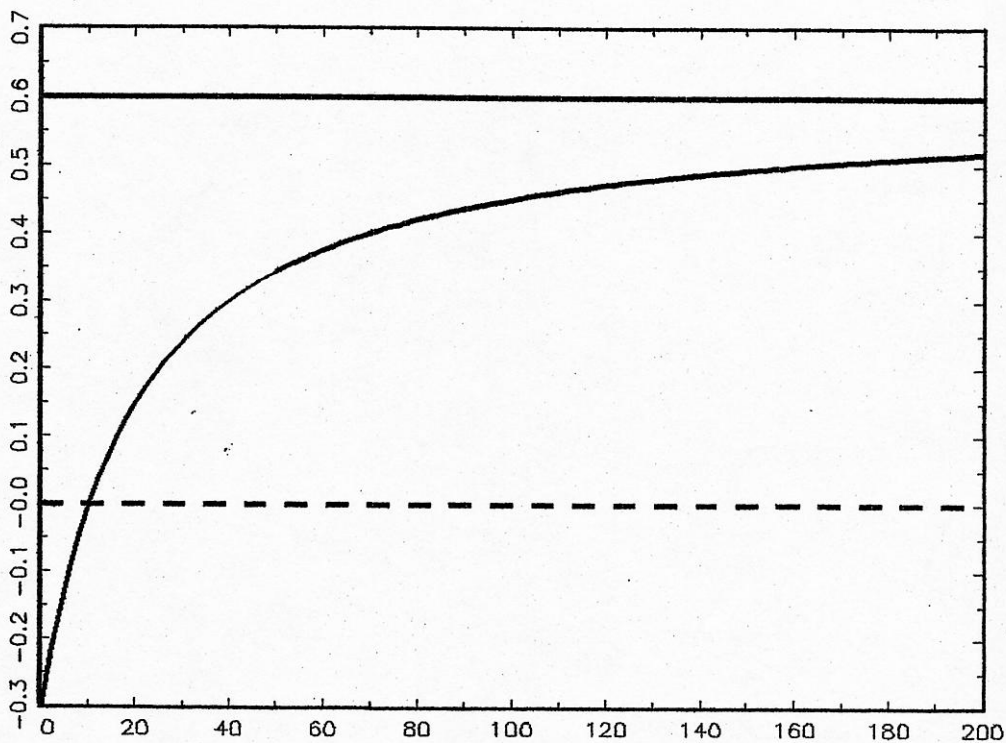
(modified exponential growth)

$$\tilde{n} = \frac{\theta\mu}{\lambda - \mu} \text{ unstable equilib.}$$

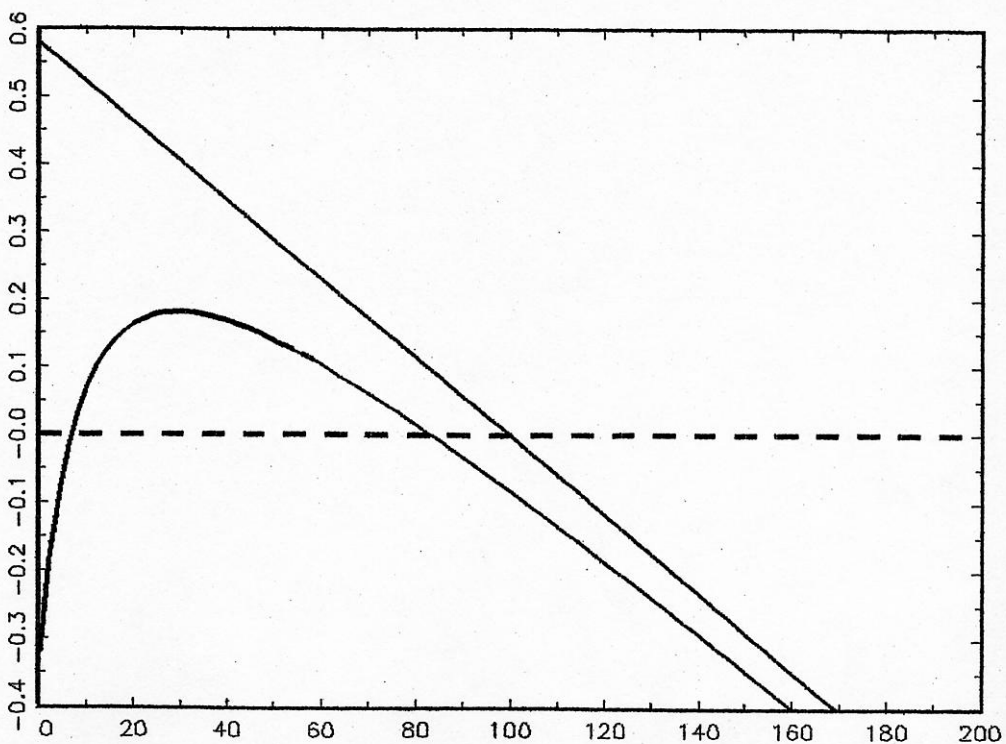
$$\frac{dn}{dt} = r n - \frac{r}{k} n^2 - \frac{\lambda\theta}{\theta + n} n$$

(modified logistic growth)

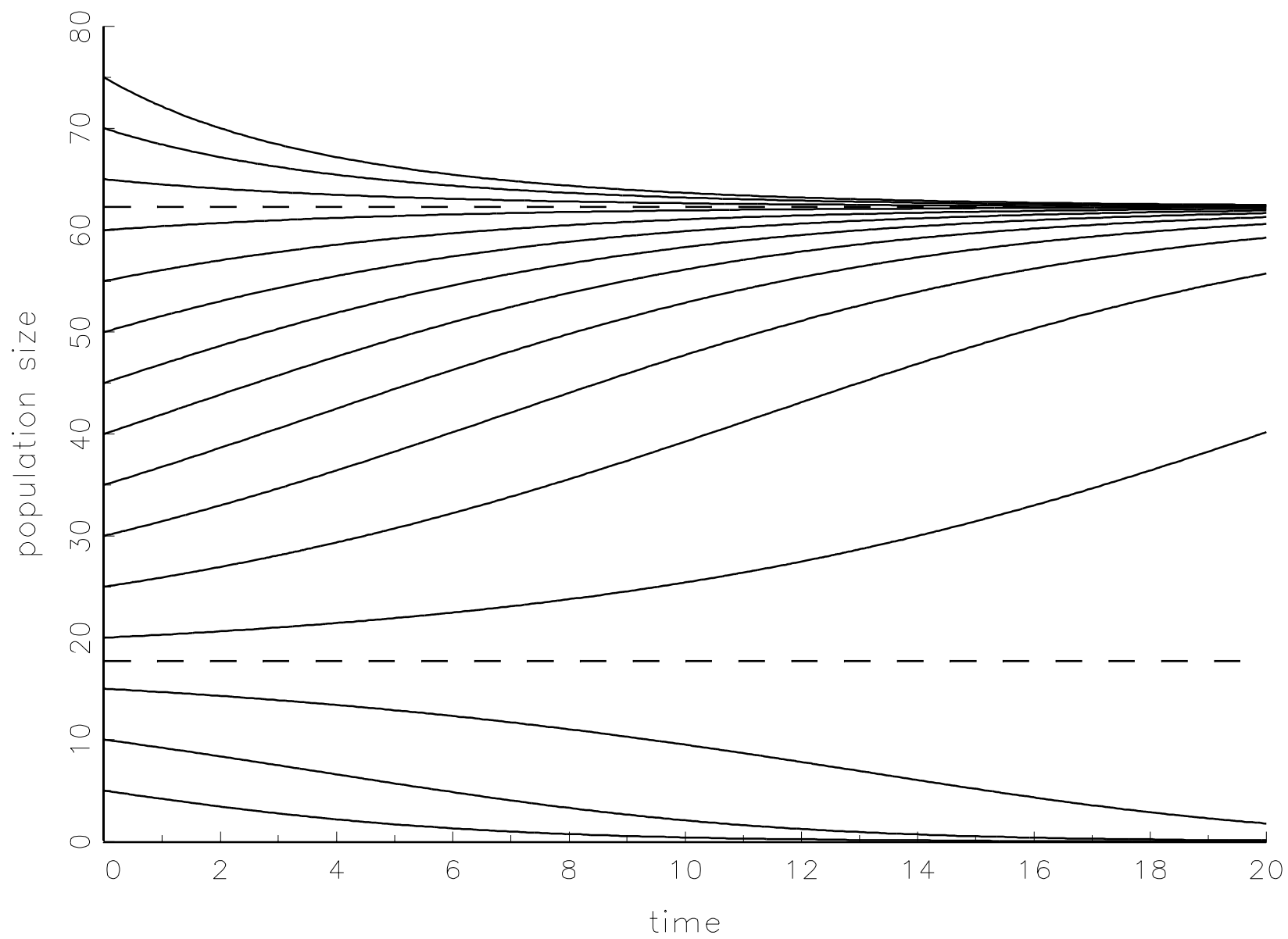
$$\frac{1}{n} \frac{dn}{dt}$$



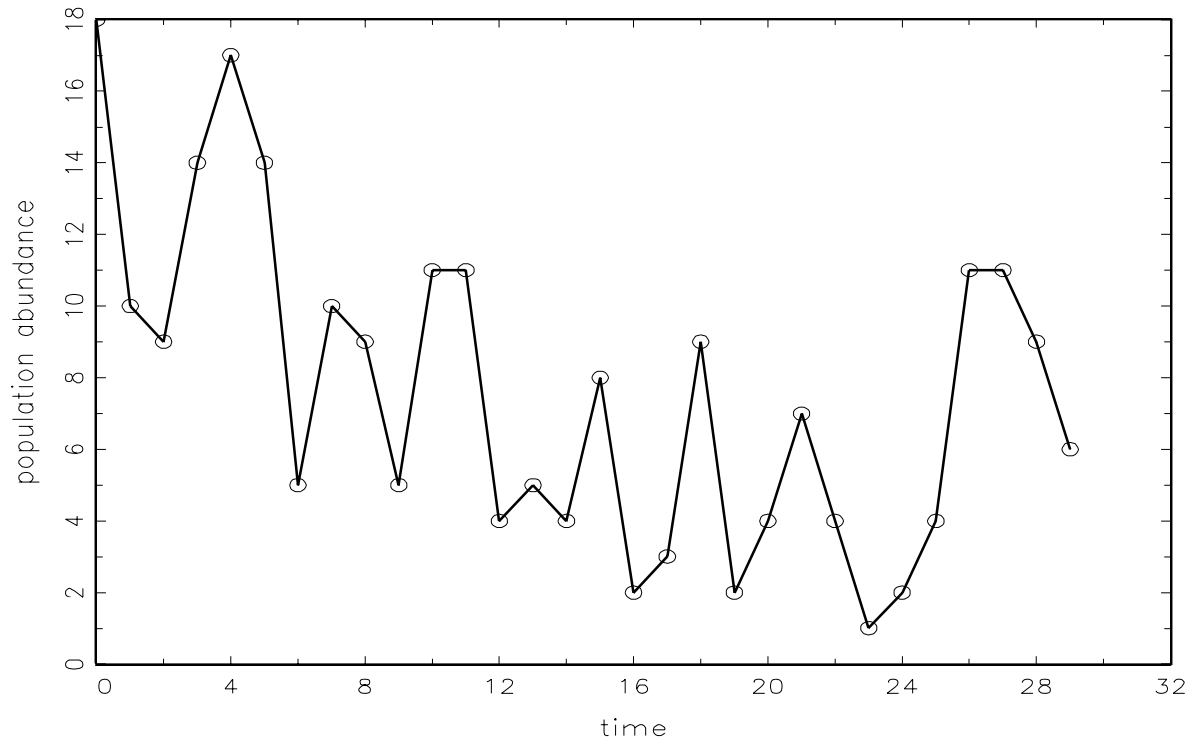
$$\frac{1}{n} \frac{dn}{dt}$$



$n$



# **variability in populations**



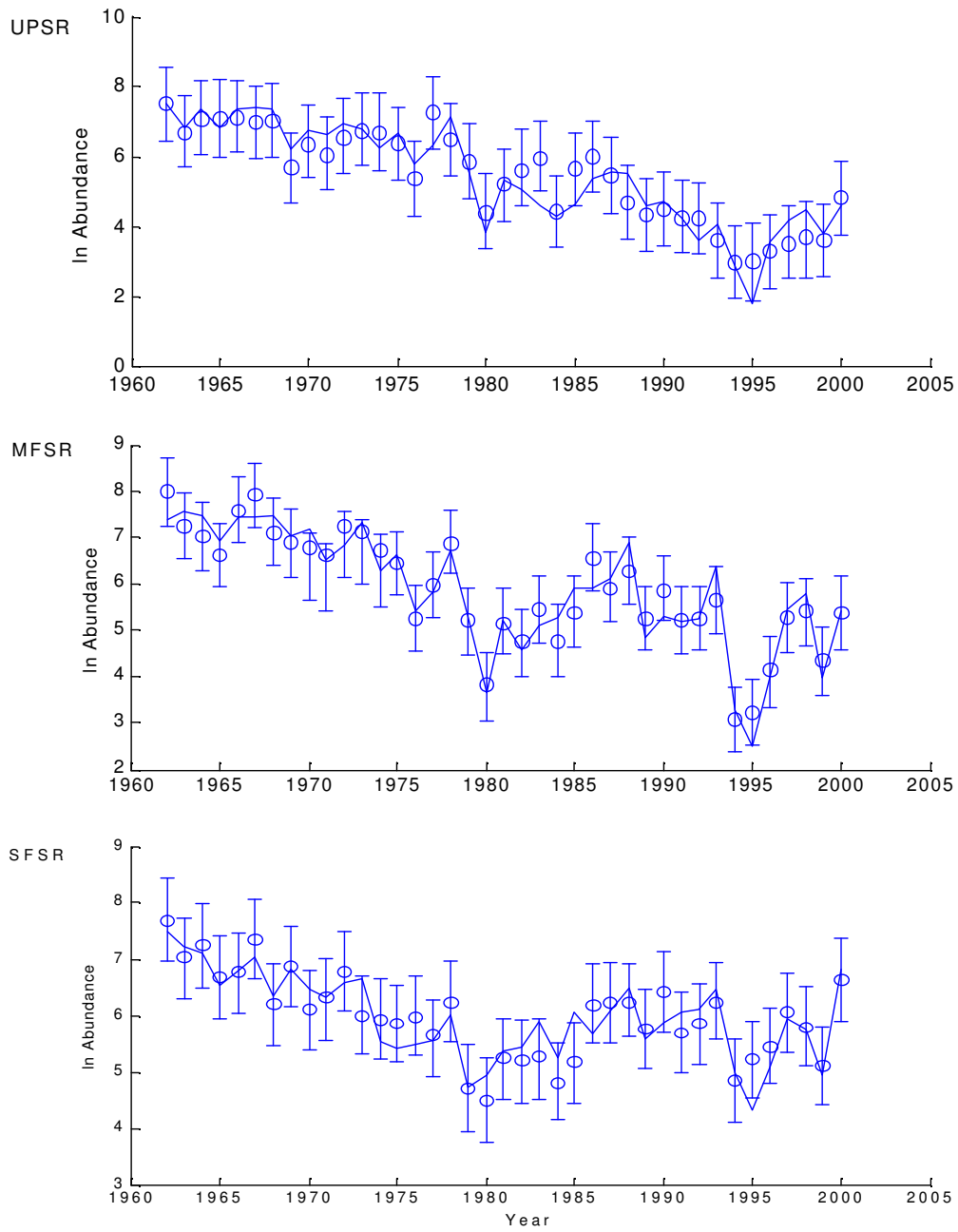


Figure 3: Annual population redd counts ( $\log_e$ ) and estimates from selected models ( $\circ$ ), with bootstrapped one-step 95% PI.

# stochastic models

*diffusion process*: a general stochastic version of

$$dn = m(n)dt$$

A DP is in the form

$$dN_t = m(N_t)dt + \sqrt{v(N_t)} dW_t,$$

where:

$N_t$  is population abundance at  
time  $t$  (random process;  
continuous function of time),

$dW_t \sim \text{normal}(0, dt)$

$m(n)$  is the infinitesimal mean  
("skeleton")

$v(n)$  is the infinitesimal variance



*ex.*  $v(n) = \alpha n$  demographic  
variability

$v(n) = \beta n^2$  environmental  
variability

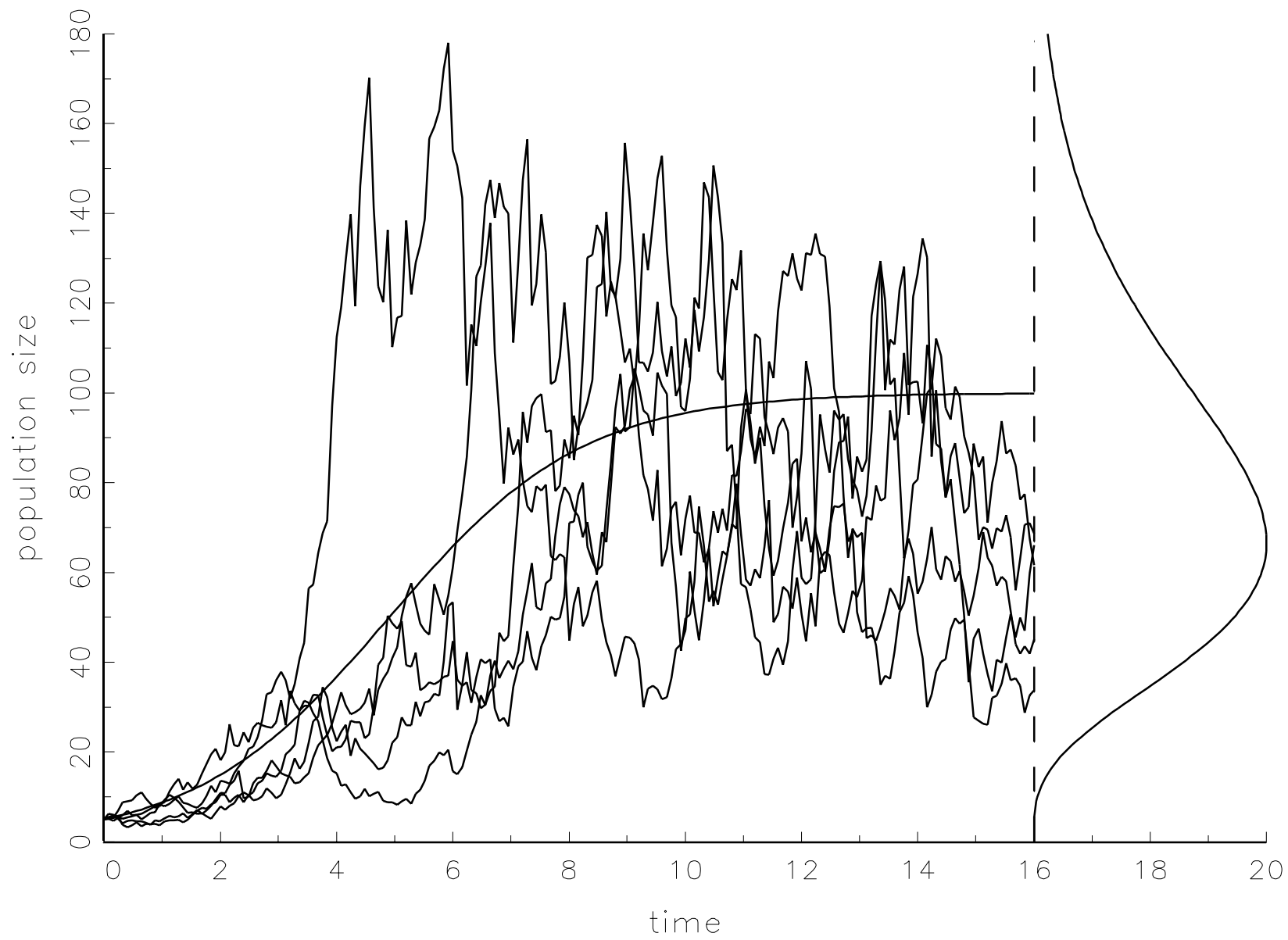
$v(n) = \alpha n + \beta n^2$  both

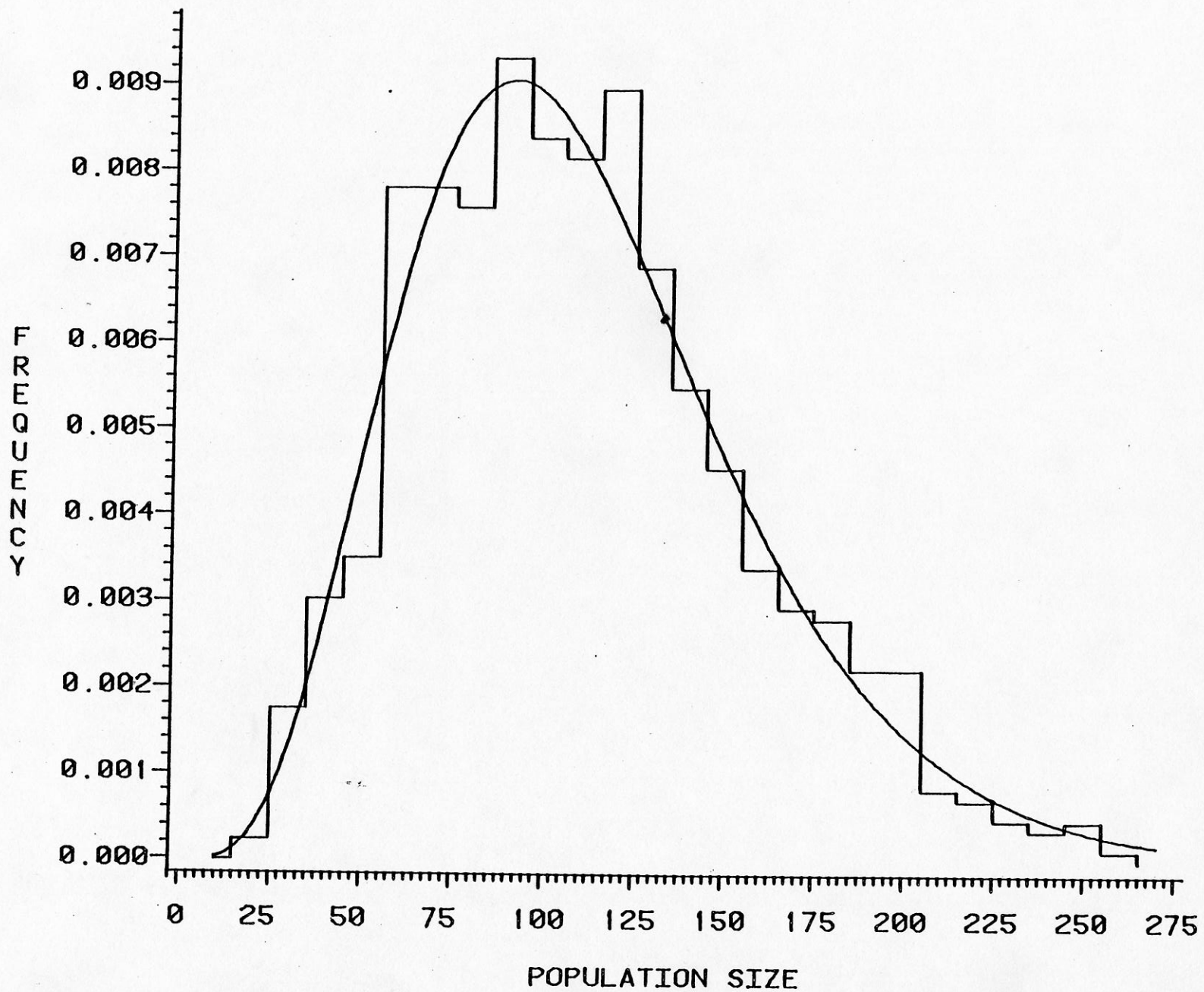
## DP conveniences

generality (approximates many  
types of stochastic processes)

tractability (pencil-and-paper  
formulas)

continuous (like the  
deterministic versions)





# First passage probability

$\xi(n; a, b)$  probability that the population first reaches size  $a$  before reaching size  $b$ , starting at  $n$ , where  $0 < a \leq n \leq b$

$$\xi(n; a, b) = \frac{\int_n^b \exp[-\phi(x)] dx}{\int_a^b \exp[-\phi(x)] dx}$$

where

$$\phi(x) = 2 \int \frac{m(x)}{v(x)} dx$$

Properties:

$$\xi(n; a, b) = 1 \text{ when } n = a$$

$$\xi(n; a, b) = 0 \text{ when } n = b$$

$\xi(n; a, b)$  is strictly monotone decreasing between  $a$  and  $b$

(Goel and Richter-Dyn 1974 catalogue many such formulas for DPs)

*Result.* If an inflection point in  $\xi(n; a, b)$  occurs at a point  $\tilde{n}$ , then  $\tilde{n}$  is a point where  $m(n)$  changes sign, and  $\tilde{n}$  is a solution to

$$m(\tilde{n}) = 0 .$$

Conversely, if  $\tilde{n}$  is a solution to  $m(\tilde{n}) = 0$ , and  $m(n)$  changes sign at  $\tilde{n}$ , then an inflection point in  $\xi(n; a, b)$  occurs at  $\tilde{n}$  (Dennis 2002 *Oikos*).

*Proof.* Differentiate twice.

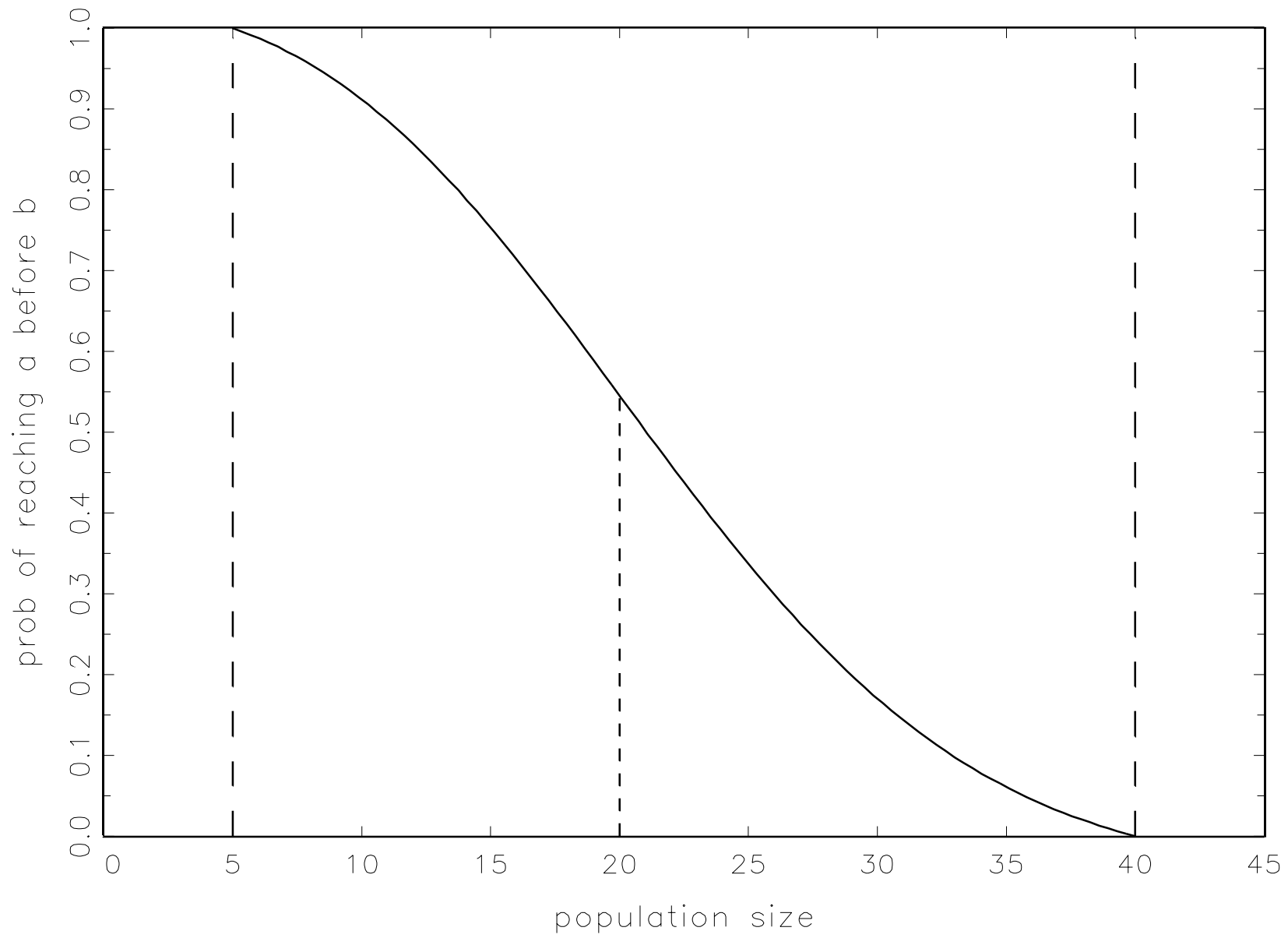
(An inflection point in  $\xi(n; a, b)$  is a point where the sign of the second derivative changes.)

In other words, stable and unstable equilibria in the skeleton correspond to inflection points in the first passage probability, and vice versa

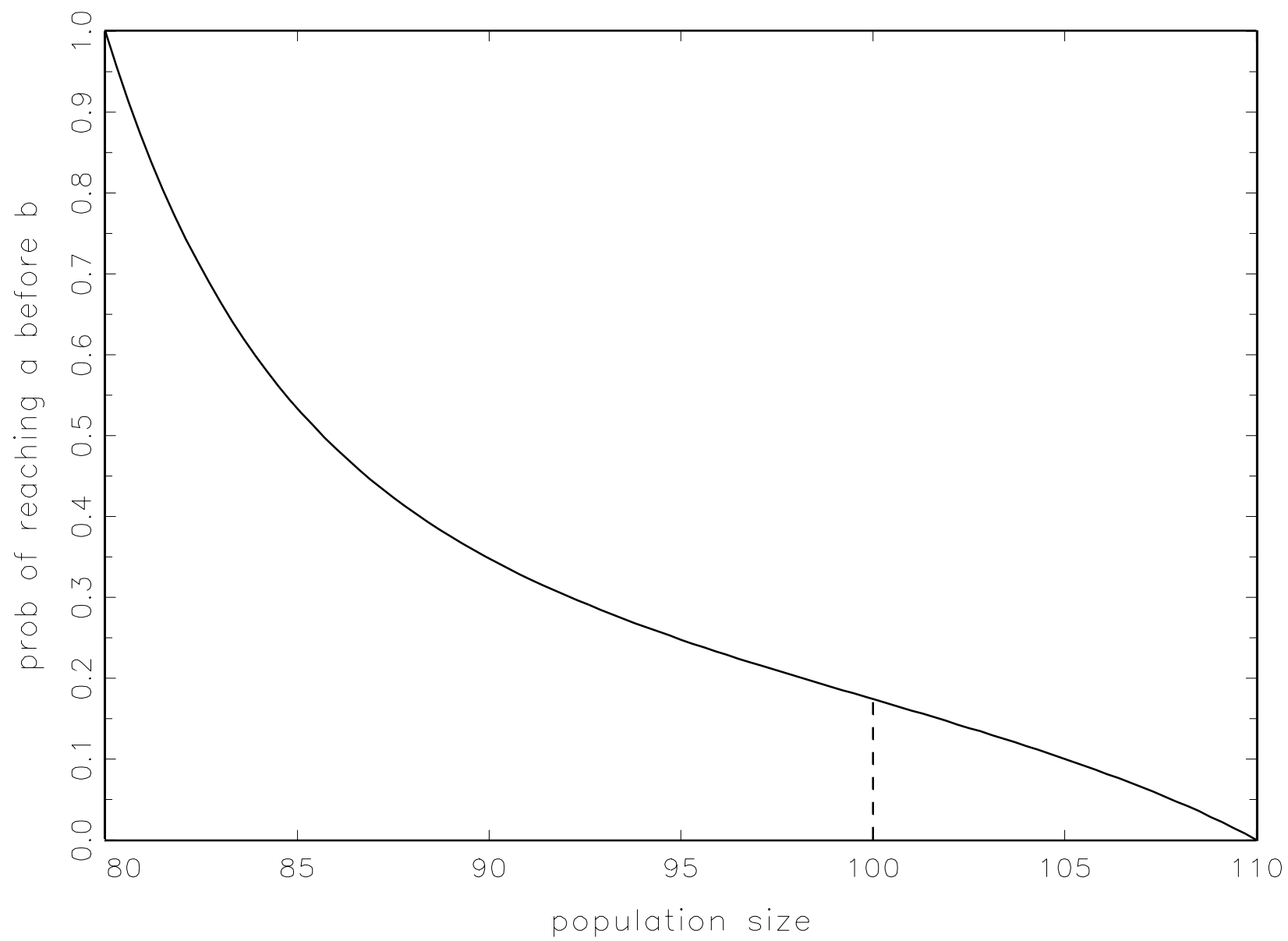


## *Notes*

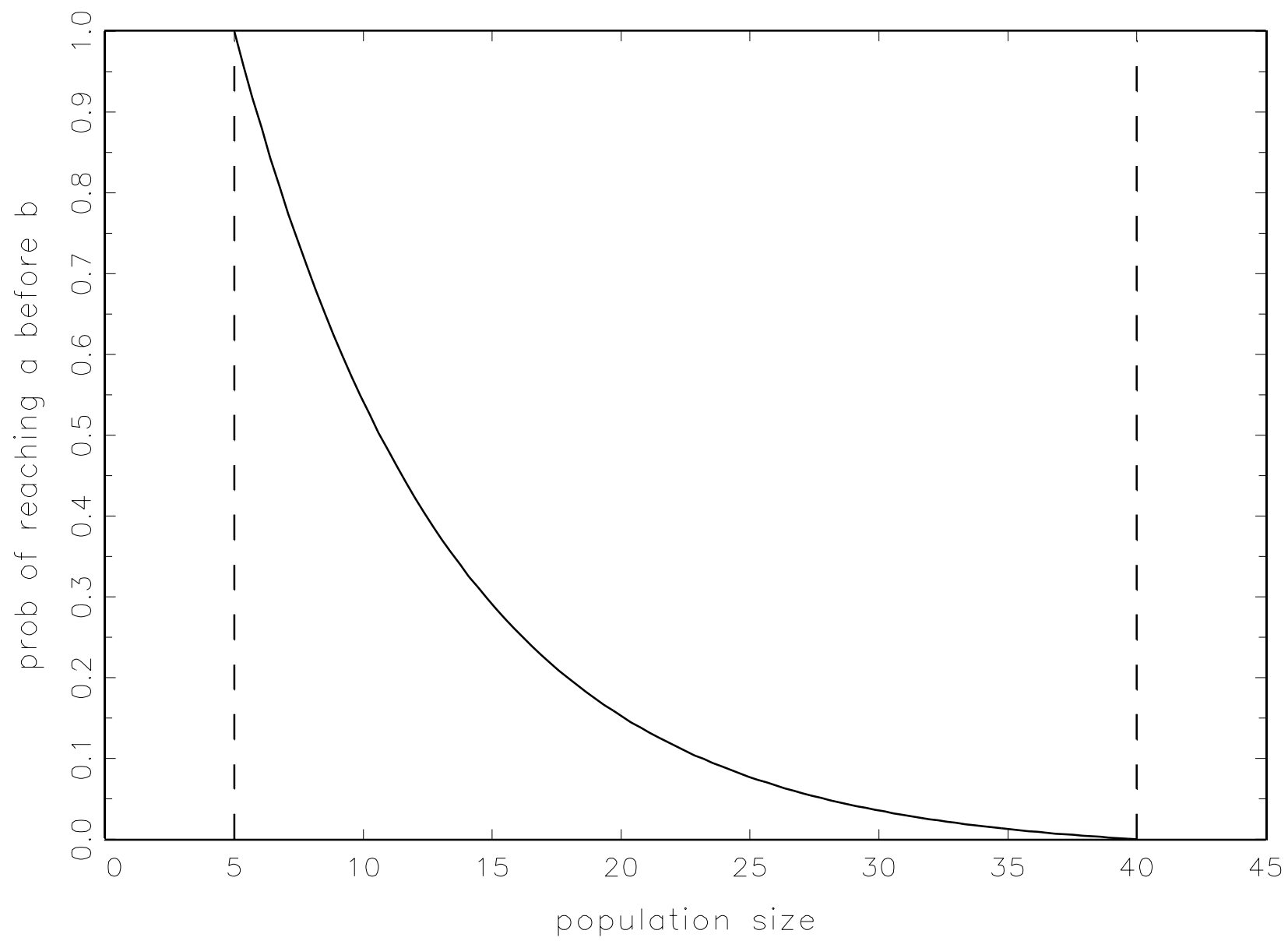
1. If  $\tilde{n}$  is a locally unstable equilibrium, then  $\xi$  changes locally at  $\tilde{n}$  from concave down ( $\cap$ ) to concave up ( $\cup$ )



2. If  $\tilde{n}$  is a locally stable equilibrium, then  $\xi$  changes locally at  $\tilde{n}$  from concave up ( $\cup$ ) to concave down ( $\cap$ )



3. If  $m(n)$  is positive throughout the interval  $a < n < b$ , then  $\xi(n; a, b)$  is concave up throughout the interval



4. The form of  $v(n)$  does *not* affect the location of the inflection points in the first passage probability. Adding or intensifying demographic noise, environmental noise, or both increases  $\xi$  but does not alter the qualitative curvature of  $\xi$ .

In particular, pure demographic noise does not produce any “threshold”-style behavior of extinction risk. Rather, such thresholds in viable population size probably point to underlying density dependent forces.

Second derivative of  $\xi$  is related to

$$\frac{m(n)}{v(n)}$$

As  $v(n)$  increases (i.e. increasing stochasticity), the curvature of  $\xi$  decreases, and inflection points are not as abrupt



# Demographic stochasticity

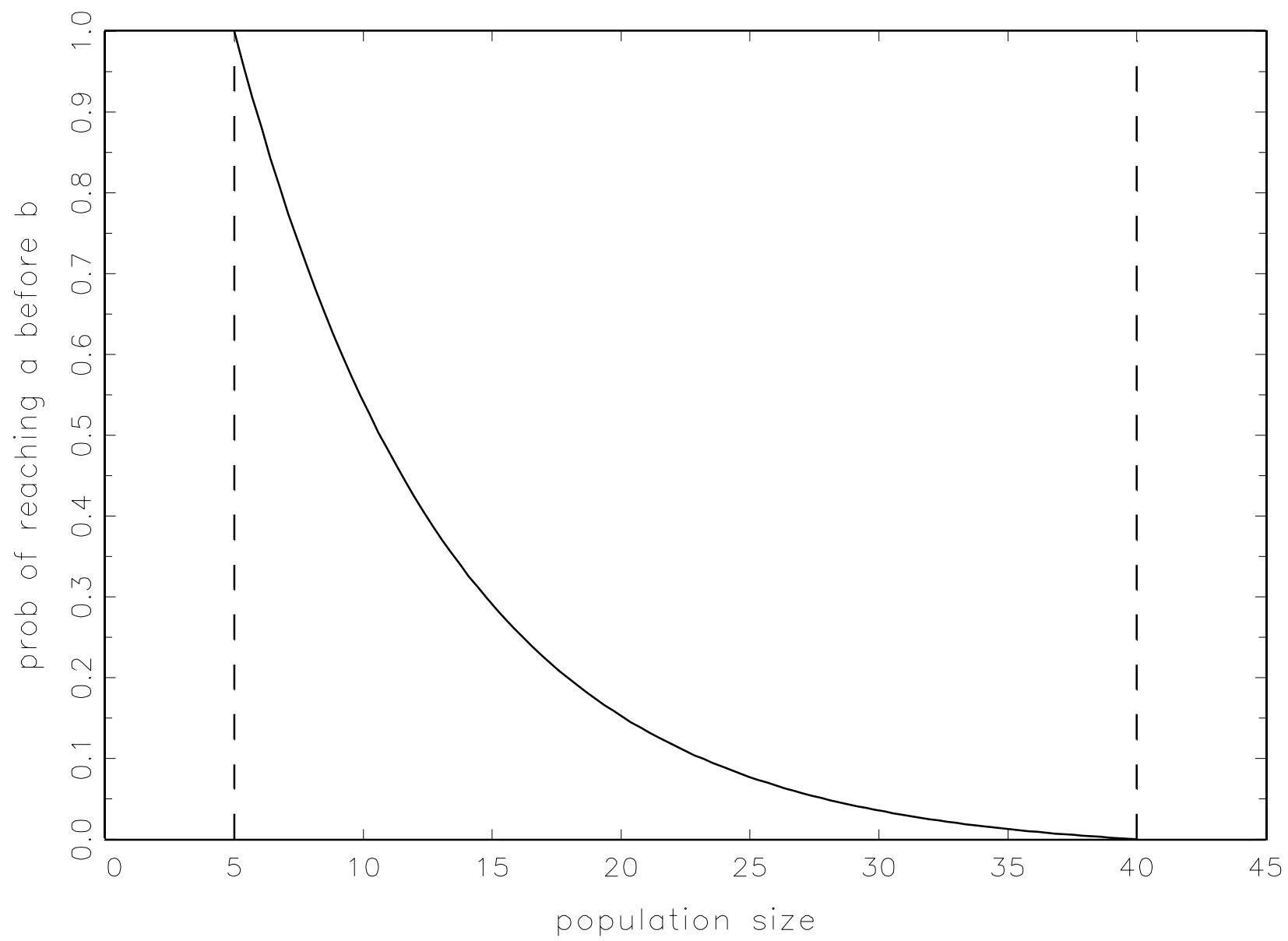
ex. exponential growth

$$m(n) = \lambda n - \mu n$$

$$v(n) = \alpha n$$

$$\xi(n; a, b) = \frac{e^{-cn} - e^{-cb}}{e^{-ca} - e^{-cb}}$$

where  $c = 2(\lambda - \mu)/\alpha$



Probability of reaching zero ( $a \rightarrow 0, b \rightarrow \infty$ ) is

$$\xi(n; 0, \infty) = e^{-cn}$$

note:  $f(x) = ce^{-cx}$  is the pdf of an exponential probability distribution, and

$$\begin{aligned}\xi(n; 0, \infty) &= \int_n^{\infty} f(x) dx \\ &= \mathbf{P}(X > n)\end{aligned}$$

is the tail probability of the distribution

# Allee effect plus demographic stochasticity

$$m(n) = \lambda n \frac{n}{\theta+n} - \mu n$$

$$v(n) = \alpha n$$

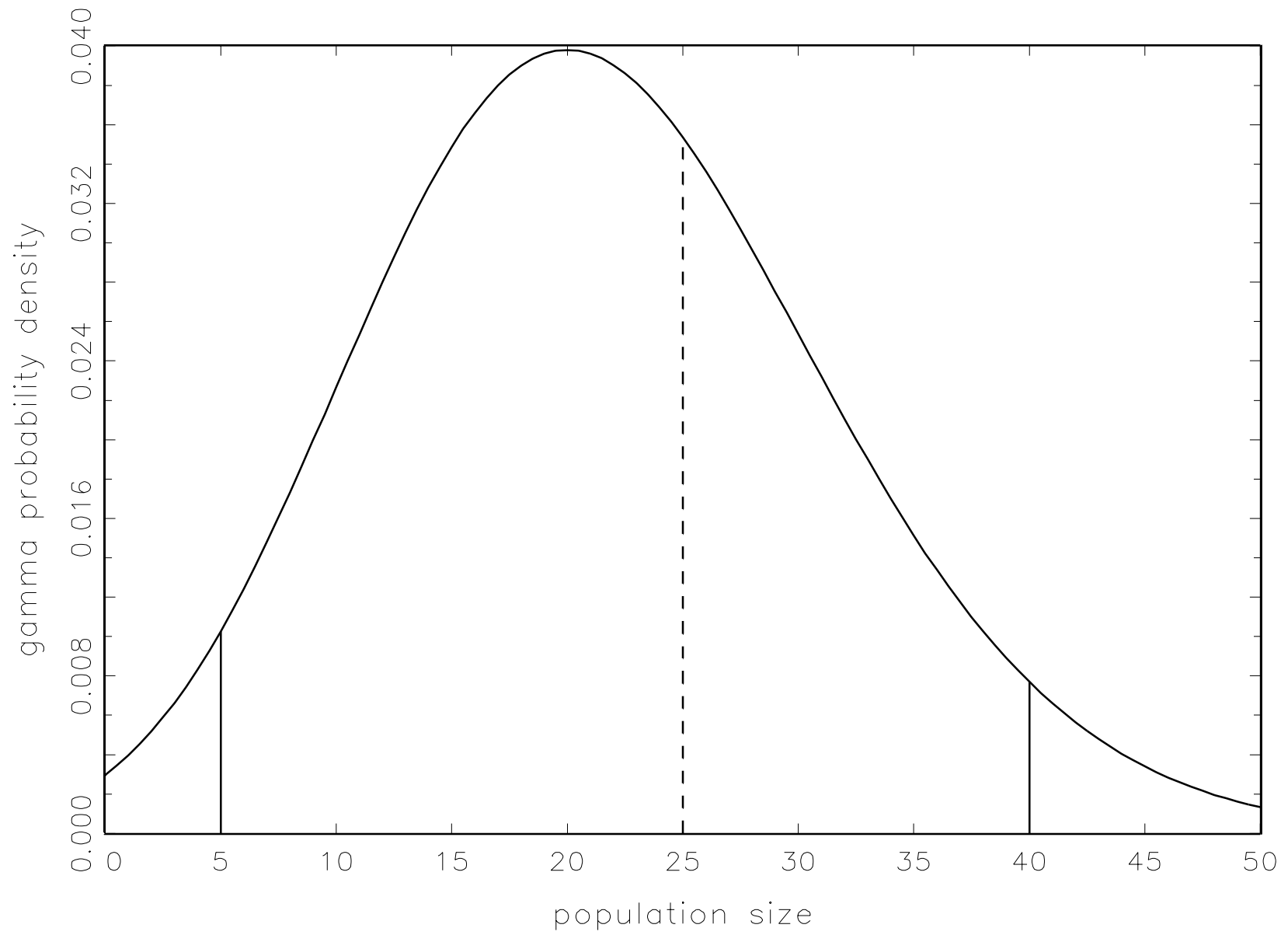
$$\xi(n; a, b) = \frac{F(b+\theta; p, q) - F(n+\theta; p, q)}{F(b+\theta; p, q) - F(a+\theta; p, q)}$$

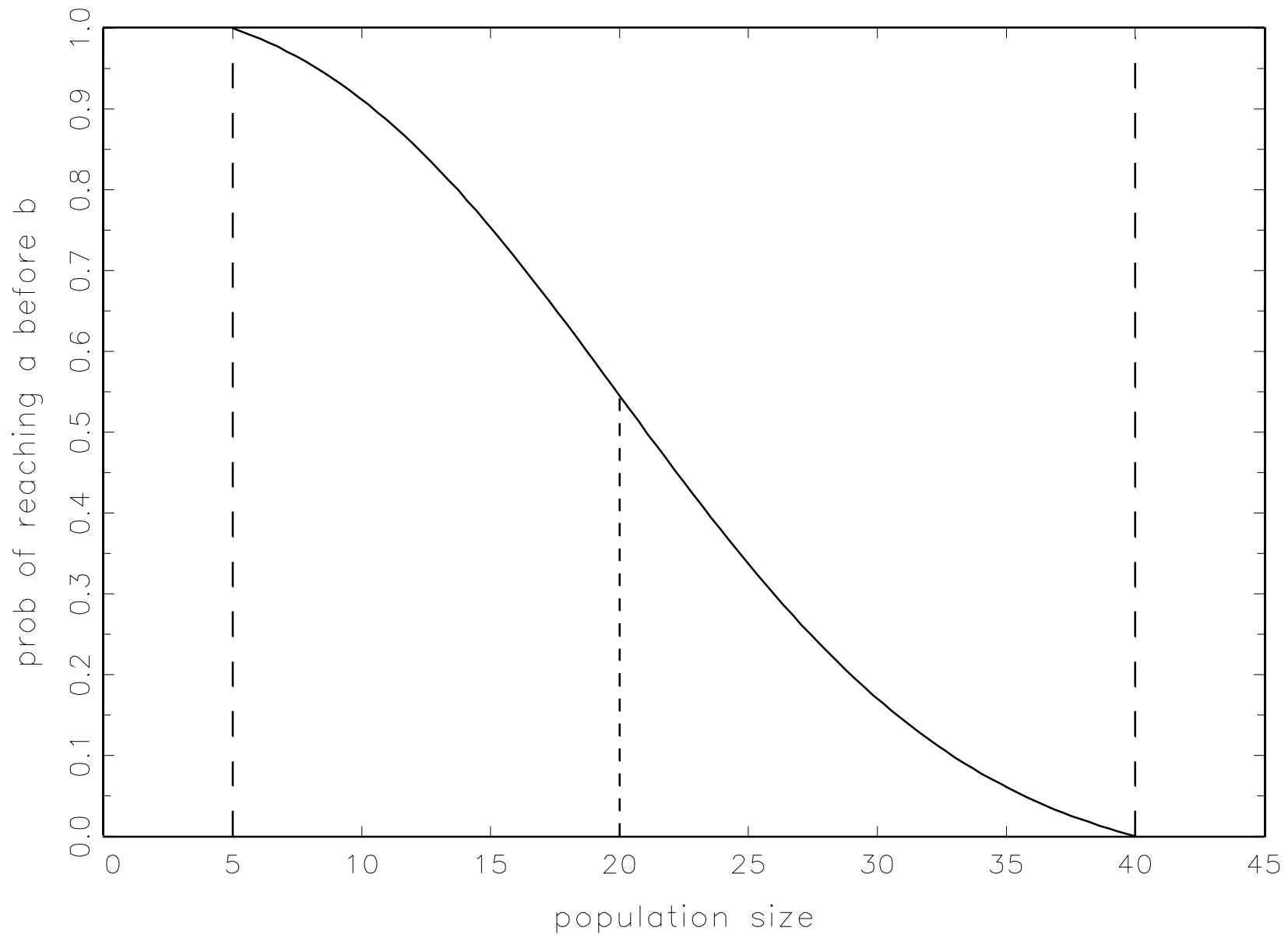
where

$$F(z; p, q) = \int_0^z \frac{q^p}{\Gamma(p)} x^{p-1} e^{-qx} dx$$

is the cdf of a gamma probability distribution

$$(p = (2\lambda\theta/\alpha) + 1, q = 2(\lambda - \mu)/\alpha)$$





Probability of reaching zero is

$$\xi(n; 0, \infty) = \frac{1 - F(n + \theta; p, q)}{1 - F(\theta; p, q)}$$

# Upper stable equilibrium

ex. logistic + demographic

$$m(n) = rn - (r/k)n^2$$

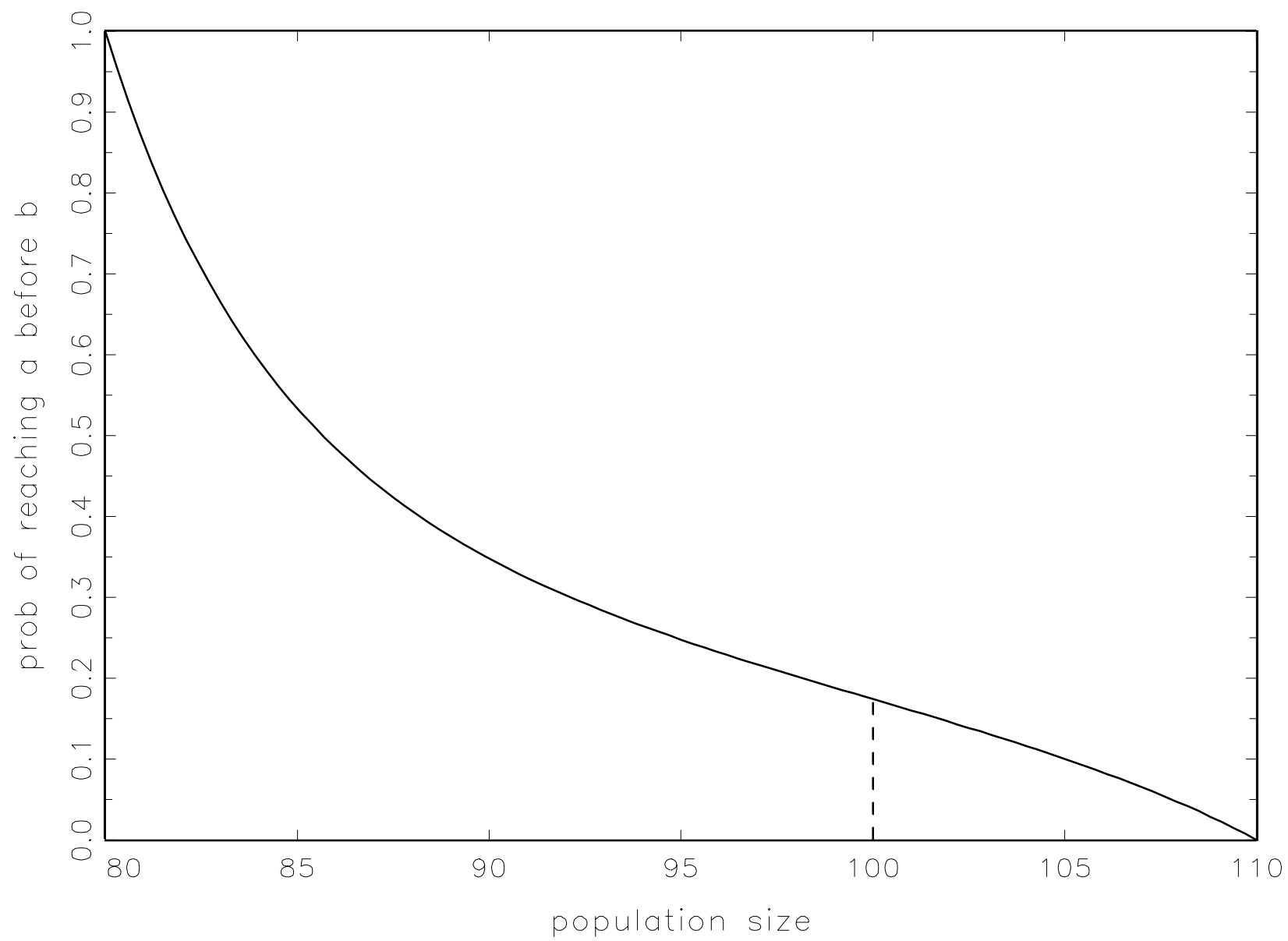
$$v(n) = \alpha n$$

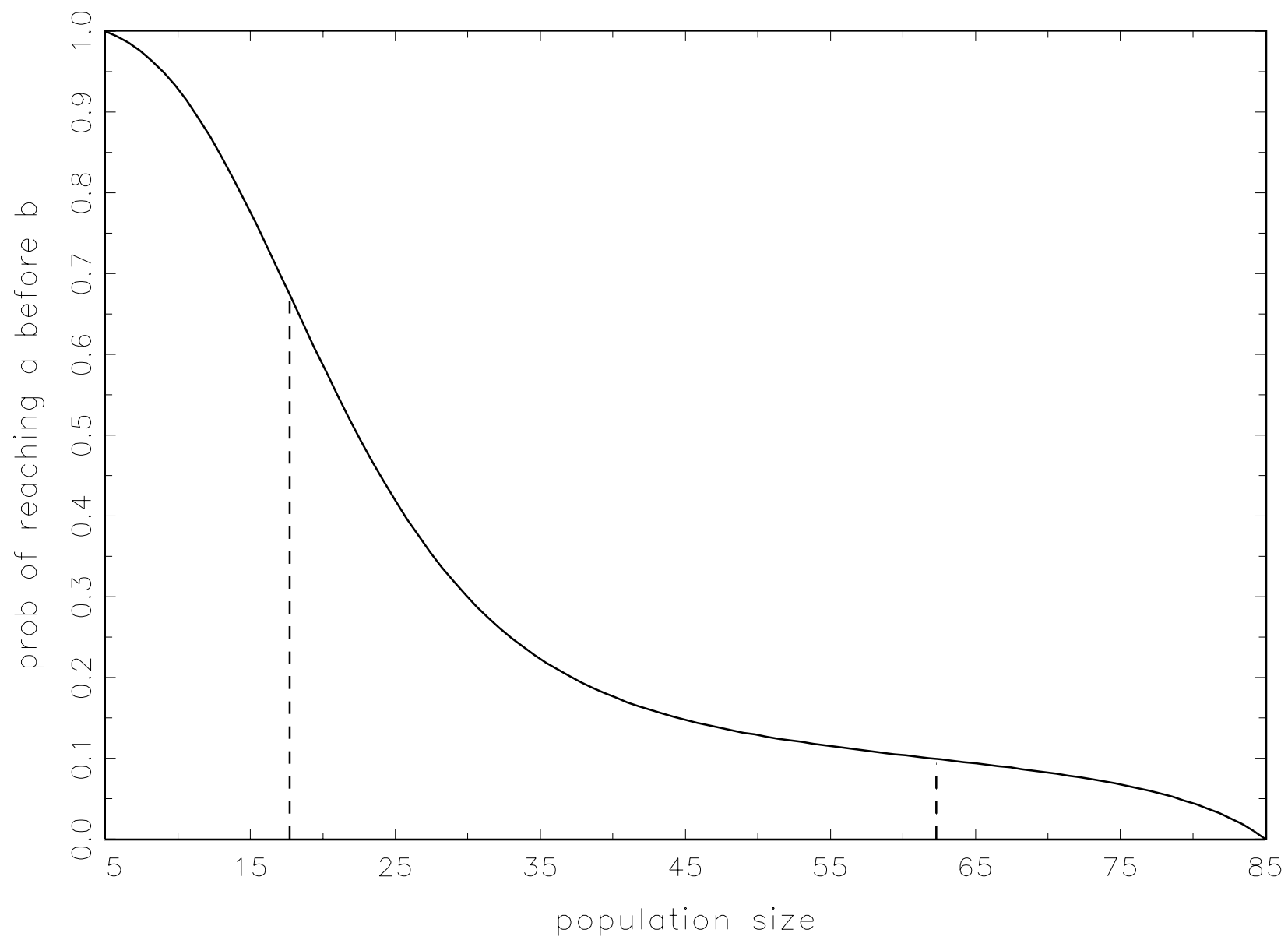
Allee, logistic, + demographic

$$m(n) = rn - \left(\frac{r}{k}\right)n^2 - \frac{\lambda\theta n}{\theta+n}$$

$$v(n) = \alpha n$$







# Discussion

Expected consequence of Allee effects: thresholds in success of species translocations and introductions, and thresholds in extinctions

Stochasticity, in and of itself, is not expected to cause threshold-like behavior in population viability. Instead, stochasticity will reduce the abruptness of thresholds

Beirne (1975 *Can. Entomol.*) — success of biological control agents for insect pests depended sharply on releasing adequate numbers

Griffith et al. (1989 *Science*) — logistic regression of success of species translocation efforts (as a function of numbers released)

Berger (1990 *Conserv. Biol.*) — populations of bighorn sheep winking in and out of existence throughout the mountain west USA; those above a critical size tended to be more viable

Hopper and Roush (1993 *Ecol. Entomol.*) —  
extensive analysis of past biological control  
introductions (follow-up of Beirne); analysis  
suggested a threshold of around 1000 individuals  
necessary to establish introduced parasitoids

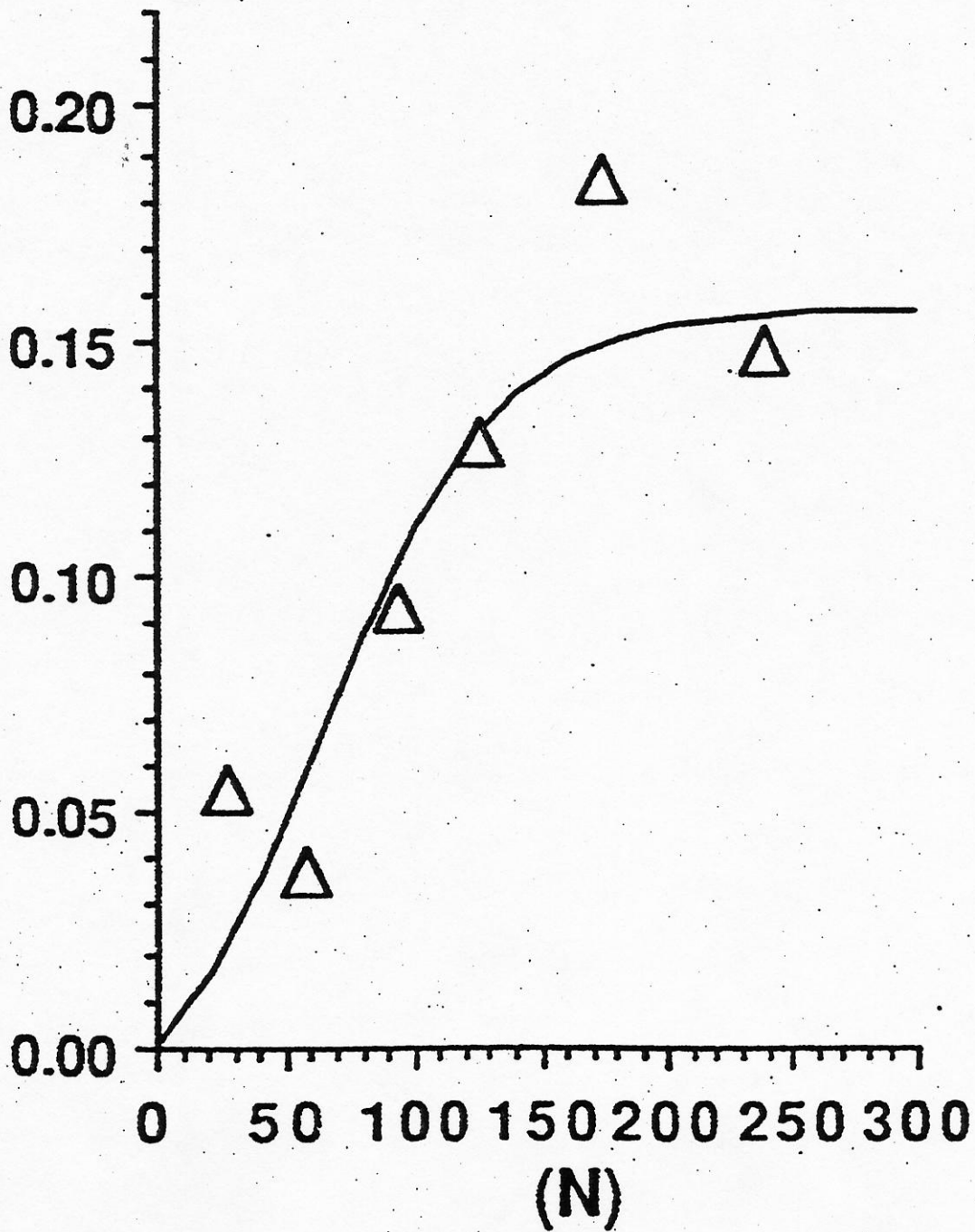
Green (1997 *J. Anim. Ecol.*) — summarized outcomes of 133 exotic bird species released in New Zealand:

> 100 individuals released  $\Rightarrow$   
83% established

< 100 individuals released  $\Rightarrow$   
21% established

Pimm (1991 *The Balance of Nature?*) — presents graph from an (as yet) unpublished study of game-bird introductions (Witteman and Pimm unpublished)

# Propagule size (N)



The four “extinction vortices” (ways in which the chance of extinction is exacerbated by small population sizes, creating a vicious cycle from which recovery is difficult) Gilpin and Soulé (1986 in Soulé, ed. *Conservation Biology: The Science of Scarcity and Diversity*):

- demographic variability
- fragmentation
- loss of fitness from reduced genetic heterozygosity
- loss of evolutionary responsiveness from reduced heterozygosity



## The fifth extinction vortex: Allee effects



Warder Clyde Allee 1885-1955

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[http://www.cnr.uidaho.edu/fishwild  
/bdennis.htm](http://www.cnr.uidaho.edu/fishwild/bdennis.htm)

**reprints available (pdf or paper):**

Dennis, B. 2002. Allee effects and stochastic populations.  
*Oikos* 96:389-401

Dennis, B. 1989. Allee effects: population growth, critical  
density, and the chance of extinction. *Natural Resource  
Modeling* 3:481-538

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