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EXTINCTION AND WAITING TIMES IN BIRTH-DEATH PROCESSES: APPLICATIONS TO ENDANGERED SPECIES AND INSECT PEST CONTROL

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SUMMARY. Stochastic birth-death processes as models of sexually reproducing populations are discussed, with emphasis on the role of familiar univariate statistical distributions. Models of mating frequency in endangered species and insect pest populations are proposed. The effects on reproduction of a paucity of matings are analyzed with respect to waiting times and extinction probabilities in stochastic population growth models and compared to deterministic cases. The probabilities of extinction in the stochastic models are the tails of familiar discrete probability distributions, with the lower critical population density corresponding to the mode of the distribution. Mating limitation of population growth produces extinction probabilities identical to those produced by constant-rate population harvesting. Distributional properties of extinction probabilities in birth-death processes are discussed with reference to weighted distributions, power series distributions, and generating functions.

KEY WORDS. extinction, birth-death processes, endangered species, insect pests, mating frequency, negative binomial, Poisson, binomial, waiting time.

1. INTRODUCTION

The evolutionary advantages of sexual reproduction are the subject of much debate among biologists (e.g., Williams, 1975). A quite obvious disadvantage of sexuality, however, has been somewhat neglected: namely, "it takes two to tango." An obligate sexual organism must encounter a fertile member of the opposite

sex to reproduce (in the case of many hermaphroditic organisms such as snails, any fellow species member will suffice). A species' survival at very low densities may be tenuous due to the uncertainty of mates finding each other (Allee, 1938; Andrewartha and Birch, 1954).

Entomologists routinely exploit this "copulatory imperative" for controlling various insect pest populations at high as well as low densities. Mating in such populations can often be disrupted by releasing large numbers of sterilized males (Braumhover *et al.*, 1955; Steiner *et al.*, 1970), or inundating an infested area with the pest species' chemical sex attractant (pheromone) (Sower and Whitmer, 1977; Richerson, Brown, and Cameron, 1976).

Mathematical models of mating and growth in rare populations are themselves rare (Volterra, 1938; Philip, 1957; Mosimann, 1958). Few models of the sterile male technique have been proposed as well (Knipling, 1955; Costello and Taylor, 1975; Prout, 1978). The mathematical perspective in these models tends to be deterministic (but see Costello and Taylor, 1975). Sexual reproduction, however, would seem a natural topic for a stochastic approach.

This paper discusses stochastic birth-death processes as models of sexually reproducing populations, with emphasis on the role of familiar univariate statistical distributions. Section 2 presents birth process models of mating frequency in endangered species or pest populations yielding several traditional probability distributions. In section 3, deterministic population growth models are compared to their stochastic birth-death processes counterparts. Here, the effects of a paucity of mating encounters on reproduction are analyzed with respect to waiting times and extinction probabilities. The tails of familiar discrete probability distributions emerge in a novel context as extinction probabilities. The "critical density" (the lower point where births in the population cease compensating for deaths) acquires an interesting meaning in the stochastic models. Mating limitation of population growth is seen to have effects similar to harvesting the population. Finally, section 4 catalogues various additional properties of extinction probabilities in birth-death processes.

2. MATING FREQUENCY DISTRIBUTIONS

Stochastic fluctuations in the number of mating encounters may affect reproduction in sparse populations. The frequency of matings for a given individual female during a breeding season can be described by a discrete probability distribution as follows. Let $X(a)$ = number of matings that a female has had

after searching an effective area a . The quantity a is taken as a measure of time if females remain stationary, waiting for males to arrive. Assuming that the ratio of males to females in the population remains constant, $X(a)$ can be regarded as a stochastic, homogeneous pure birth process with a rate, $\delta(x)$, roughly proportional to the population density, n . For small n it is reasonable to assume that $\delta(x)$ is a linear function of x :

$$\delta(x) = (b + cx)n. \quad (1)$$

This birth rate accommodates a variety of biological situations. Given that a female has encountered males, she is: a) more likely to mate an additional time during a small interval Δa if $c > 0$ (aggregation); b) equally likely when $c = 0$ (random); or c) less likely if $c < 0$ (regularity or saturation). From the general solution for $\text{Pr}[X(a) = x] = p_x(a)$ in pure birth processes (Bartlett, 1978, p. 58), cases a, b, and c yield the negative binomial, Poisson, and binomial distributions, respectively (e.g. Patil and Stiteler, 1974; Boswell, Ord, and Patil, 1979):

$$p_x(a) = \binom{b/c+x-1}{x} (e^{-acn})^{b/c} (1-e^{-acn})^x, \quad x = 0, 1, 2, \dots \quad (c > 0) \quad (2)$$

$$p_x(a) = e^{-abn} (abn)^x / x!, \quad x = 0, 1, 2, \dots \quad (c = 0) \quad (3)$$

$$p_x(a) = \binom{-b/c}{x} (1-e^{-acn})^x (e^{-acn})^{(-b/c)-x}, \quad x = 0, 1, \dots, -b/c \quad (c < 0). \quad (4)$$

For many species, a female must encounter only one male during a breeding season to realize full reproductive potential. Under these circumstances, the quantity of interest is the probability of finding one or more mates:

$$\text{Pr}[X(a) \geq 1] = 1 - e^{-\beta n}. \quad (5)$$

Here $\beta = ab$ is a measure of the inherent mate-finding abilities of the species members. This mating probability was first proposed by Philip (1957), who derived it using Poisson process assumptions (case b). Mosimann (1958) provides some interesting estimates of β for box turtle populations. The expected number of females that mate, and presumably reproduce, is assumed proportional to $n(1 - e^{-\beta n})$.

For other species, a female's reproductive rate increases with actual mating frequency. The expected mating frequencies for (2), (3), and (4) above are, respectively,

$$E[X(a)] = (b/c)(e^{acn} - 1), \quad (6)$$

$$E[X(a)] = abn, \quad (7)$$

$$E[X(a)] = (-b/c)(1 - e^{-acn}) \quad (8)$$

The assumption that n is small is seen to be important in (6) and (7), for mating frequency could hardly increase indefinitely with increasing n due to biological constraints. In (8) an upper limit to mating frequency (satiation or saturation) is built in.

If the per individual reproductive rate is proportional to expected mating frequency, then (7) is essentially the mating model proposed by Volterra (1938). Volterra presumed that mating encounters between the sexes were analogous to bimolecular collisions of gas molecules. Note also that the functional dependence of (8) and (5) on n are similar. Thus, Philip's negative exponential mating function (5) could represent a mating frequency as well as a mating probability.

It is reasonable to assume that a population is not homogeneous with regard to the value of β . For instance, β might vary from individual to individual or from day to day due to difference in distances traversed, home ranges, weather factors affecting pheromone diffusion, or other random environmental factors. Heterogeneity in β can be represented by a continuous probability density, $f(\beta)$. The unconditional probability of mating is then, from (5),

$$\begin{aligned} \Pr[X(a) \geq 1 \text{ (unconditional)}] &= 1 - \int_0^{\infty} e^{-\beta n} f(\beta) d\beta \\ &= 1 - g(n). \end{aligned} \quad (9)$$

The function $g(n)$ is the Laplace transform of $f(\beta)$, and occurs as a simple example of "marking" a renewal stream with a Poisson process (Rade, 1972).

The exponential density, $f(\beta) = \theta e^{-\theta\beta}$, is a likely candidate for the form of $f(\beta)$, as it describes a wide variety of stochastic phenomena without entailing a net increase in the number of model parameters. The probability of mating, from (9), is a rectangular hyperbola in n :

$$\Pr[X(a) \geq 1] = n/(\theta + n). \quad (10)$$

The parameter θ is the population density at which the probability of mating is $1/2$.

We might surmise that releasing a pheromone into a pest population has the effect of increasing θ . The insects' chemical communication system becomes disrupted with high concentrations of pheromone in the air, making it difficult for mates to locate each other. Specific quantitative relationships between θ and pheromone concentrations have not been studied, however.

We note that any other probability density specified as the form for $f(\beta)$ in (9) yields a mating probability curve shaped similar to (10) as a function of n . In particular, (9) will not be sigmoid unless $f(\beta)$ depends on n . This stems from the complete monotone property of Laplace transforms (Feller, 1966, p. 415).

The hyperbolic mating function (10) curiously arises in an entirely different context as a model of the sterile male method of pest control. In this method, large numbers of males are reared and sterilized with radiation or chemicals. They are then released and maintained at a density of ξ in the pest population. If the density of wild males is v_n , the probability that a female mates with a fertile (wild) male is $n/[(\xi/v) + n]$. The argument assumes the sterile males are as vigorous in mating as fertile males, the sex ratio remains constant, and the organisms have no trouble finding each other to mate. This sterile male model originated with Knippling (1955), though Kostitzin (1940) proposed a vaguely similar chance mechanism for using the hyperbola as a fertilization probability.

3. POPULATION GROWTH MODELS

3.1 Stochastic vs. Deterministic. Single species growth models in the ecological literature are customarily deterministic and continuous. The growth rate of a population is given by

$$dn/dt = \lambda(n) - \mu(n), \quad (11)$$

where n = population density (a continuous function of time), and $\lambda(n)$ and $\mu(n)$ are the instantaneous natality and mortality rates, respectively, in the population.

A stochastic approach, however, seems more appropriate for sparse populations, affording a variety of possible outcomes from a given initial population density. A stochastic model "corresponding" to the deterministic model (11) might be defined as the Markov birth-death process with birth rate $\lambda(n)$ and death rate $\mu(n)$. There are usually numerous stochastic "versions" of any deterministic model; a birth-death process has the advantage of treating n as a discrete variable. The fact that organisms come in integer packages is critical for

endangered species. Furthermore, the probability of ultimate extinction, a quantity of obvious interest, is easily computed for a birth-death process.

Three forms for $\lambda(n)$ are considered:

$$\lambda(n) = \lambda n; \quad \lambda(n) = \lambda \epsilon n^2; \quad \lambda(n) = \lambda n^2 / (\theta + n). \quad (12)-(14)$$

The first is a simple linear birth rate for a population not experiencing a mating shortage. The second, the bimolecular collisions model suggested by Volterra (1938), is the simple linear rate multiplied by a factor proportional to the expected per capita mating frequency (7). The third is the simple linear rate multiplied by the expected proportion of organisms that find mates under the hyperbolic mating function (10). A fourth birth rate based on the negative exponential function (5),

$\lambda(n) = \lambda n(1 - e^{-\beta n})$, behaves quite similarly to (14) in dynamical growth models, but tends to be less tractable.

3.2 Pure Birth Models and Waiting Times. Pure birth models set $\mu(n) = 0$ for all n . This assumption is reasonable when losses from the population are insignificant. Though decline or extinction is not possible, the effect of a mating shortage is to increase greatly the waiting time necessary for the population to reach a certain size. This is seen by examining such waiting times in both the deterministic and stochastic birth models.

The deterministic waiting time, t , required for a population of initial size m to reach a given size n is found explicitly by integrating (11):

$$t = \int_m^n [1/\lambda(u)] du. \quad (15)$$

For the three birth rates (12)-(14), we have, respectively,

$$t = (1/\lambda)[\log n - \log m], \quad (16)$$

$$t = [1/(\lambda\epsilon)][(1/m) - (1/n)], \quad (17)$$

$$t = (1/\lambda)[\log n - \log m] + (\theta/\lambda)[(1/m) - (1/n)]. \quad (18)$$

Rearranged, (16) gives the more familiar form $n = me^{\lambda t}$. In (17), $t \rightarrow 1/(m\lambda\epsilon)$ as $n \rightarrow \infty$, showing that n becomes infinite in a finite time under this model. A population's growth could thus be approximated by this model only for short time periods and low initial densities. The reciprocal of birth rate (14) in (15) is $1/\lambda(n) = 1/(\lambda n) + \theta/(\lambda n^2)$. The waiting time (18) is thus the sum of (16) and a component resembling (17). Growth in the hyperbolic mating-limited population is delayed over (16)

by an amount related to the "collisions" between the sexes.

In stochastic pure birth processes, the waiting time to reach size n from initial size m is a continuous random variable, denoted T . The expected value of T is similar to (15), except that it is found by summing, rather than integrating, the reciprocal birth rates.

$$E[T] = \sum_{k=m}^{n-1} 1/\lambda(k). \quad (19)$$

With the birth rates (12), (13), and (14), we have

$$E[T] = (1/\lambda)[\Psi(n) - \Psi(m)], \quad (20)$$

$$E[T] = [1/(\lambda\epsilon)][\Psi'(m) - \Psi'(n)], \quad (21)$$

$$E[T] = (1/\lambda)[\Psi(n) - \Psi(m)] + (\theta/\lambda)[\Psi'(m) - \Psi'(n)] \quad (22)$$

Here $\Psi(\cdot)$ is the digamma function (Abramowitz and Stegun, 1965, p. 258). Expression (20) is always slightly greater than its deterministic counterpart (16) for the same values of λ , n , and m . Noting that $d(\log n)/dn = 1/n$, we see that (21) bears the same relationship to (20) as does (17) to (16). The birth process resulting from (13) is stochastically explosive, in that there is a positive probability that the population becomes infinite in a finite time (see Feller, 1968, p. 453). Using the more realistic birth rate (14), (22) is again the sum of a simple linear component (20) and a collisions component, as was the case for (18). However, (22) is always somewhat greater than (18).

3.3 Birth-Death Models and Extinction. Models allowing the possibilities of decline and extinction are appropriate for populations experiencing significant mortality losses. For simplicity, the form of the loss rate is hereafter assumed to be $\mu(n) = \mu n$, where μ is a constant less than λ .

Population increase occurs for all initial densities under the deterministic model (11) with the simple linear birth rate (12). For either of the mating birth rates (13) and (14), an equilibrium, denoted \bar{n} , typically exists where $\lambda(\bar{n}) = \mu\bar{n}$. The equilibrium is unstable, that is, the population increases if $m > \bar{n}$. This equilibrium is termed the *critical density* in a loose analogy to the critical mass of atomic fission. Indeed, the solution trajectories of (11) using (13) as a birth rate are explosive when $m > \bar{n}$. The critical density is $\bar{n} = \mu/(\lambda\epsilon)$ using (13) and is $\bar{n} = \theta\mu/(\lambda - \mu)$ using (14).

Stochastic birth-death processes incorporating (12), (13), or (14) more reasonably allow possibilities of increase or decrease from a given initial population size. This property is particularly important for low population densities. As $\lambda(0) = 0$, zero is an absorbing state; extinction is a possible outcome of these processes.

The chance of extinction is a quantity of special interest for preserving endangered species or eradicating injurious ones. It is a well-known result from birth-death processes (e.g., Karlin and Taylor, 1975, p. 149) that the probability of extinction from an initial size m , denoted $\alpha(m)$, is

$$\alpha(m) = \left[\sum_{x=m}^{\infty} \rho(x) \right] / \left[1 + \sum_{x=1}^{\infty} \rho(x) \right], \quad (23)$$

where

$$\rho(x) = [\mu(1)\mu(2)\cdots\mu(x)] / [\lambda(1)\lambda(2)\cdots\lambda(x)], \quad (24)$$

under the condition that $\sum \rho(x)$ converges. Extinction is certain if the sum does not converge.

Observe that a discrete probability distribution can be defined by

$$\Pr[X = x] = \begin{cases} 1 / \left[1 + \sum_{k=1}^{\infty} \rho(k) \right], & x = 0; \\ \rho(x) / \left[1 + \sum_{k=1}^{\infty} \rho(k) \right], & x = 1, 2, \dots \end{cases} \quad (25)$$

The probability of extinction is seen to be the tail of this distribution:

$$\alpha(m) = \Pr[X \geq m] = \sum_{x=m}^{\infty} \Pr[X = x]. \quad (26)$$

Ecologists have adopted the simple linear birth-death process incorporating (12) as a stochastic model of a species colonizing a new environment such as an island (MacArthur and Wilson, 1967; Crowell, 1973). The birth-death process incorporating (14) is a slightly modified version of the pest control model given by Costello and Taylor (1975). The probabilities of extinction for the three birth-death processes incorporating (12), (13), and (14), are, respectively, the tails of geometric, Poisson, and negative binomial distributions:

$$\alpha(m) = \sum_{x=m}^{\infty} (1-\mu/\lambda)(\mu/\lambda)^x = (\mu/\lambda)^m, \quad (27)$$

$$\alpha(m) = \sum_{x=m}^{\infty} e^{-(\mu/\lambda\varepsilon)} (\mu/\lambda\varepsilon)^x / x! = \gamma(m, \mu/\lambda\varepsilon) / \Gamma(m), \quad (28)$$

$$\alpha(m) = \sum_{x=m}^{\infty} \binom{\theta + x}{x} (1 - \mu/\lambda)^{\theta+1} (\mu/\lambda)^x. \quad (29)$$

In (28), $\gamma(\cdot, \cdot)$ represents the incomplete gamma function (Gradshetyn and Ryzhik, 1965, p. 940).

In (27), $\alpha(m)$ as a function of m decreases in the characteristic geometric fashion. If $\lambda\varepsilon > \mu$, (28) as a function of m resembles (27) in shape. If $\lambda\varepsilon < \mu$, (28) acquires a declining sigmoid shape with the inflection point, \bar{m} say, occurring at $\bar{m} \approx \mu/\lambda\varepsilon$. This quantity corresponds to the mode of the Poisson probabilities in (28) and is also the population density at which $\lambda(\bar{m}) = \mu$. The function (29) also displays the declining sigmoid shape for values of $\theta > (\lambda - \mu)/\mu$; the extinction probabilities for this mating model are greatly increased over those in (27) when θ represents a sizable fraction of m . The inflection point of (29) occurs at $\bar{m} \approx \theta\mu/(\lambda - \mu)$, corresponding to the mode of the negative binomial probabilities and to the point where $\lambda(\bar{m}) = \mu$. The quantity \bar{m} for both (28) and (29) is the stochastic counterpart to the critical density of the deterministic models.

Setting $\theta = 0$ in birth rate (14) of course recovers birth rate (12). The geometric distribution in (27) follows as a special case of the negative binomial in (29). Additionally, (29) is equivalent to the left tail of a binomial distribution when θ is an integer:

$$\alpha(m) = \sum_{x=0}^{\theta} \binom{m + \theta}{x} (1 - \mu/\lambda)^x (\mu/\lambda)^{m+\theta-x}. \quad (30)$$

3.4 Relationship to Harvesting Models. Curiously, the mating models incorporating (13) and (14) are identical to population harvesting models with respect to their extinction probabilities. Consider a population with a simple linear birth rate (12) that is harvested at a constant (stochastic) rate μ/ε . Thus, $\lambda(n) = \lambda n$ and $\mu(n) = \mu/\varepsilon$. The probability of extinction for this process is exactly (28). Also, consider a population growing according to a simple linear birth-death process that is harvested constantly at rate $\mu\theta$. Thus, $\lambda(n) = \lambda n$ and $\mu(n) = \mu n + \mu\theta$. The probability of extinction for this second process is exactly (29). Failure to mate essentially represents removal of population members from the reproductive process.

It is interesting to further consider the effect of harvesting on a mating-limited population. Letting

$\lambda(n) = \lambda n^2 / (\theta + n)$ and $\mu(n) = \mu n + \gamma$, where γ is a constant stochastic harvesting rate, we obtain the tail of a probability distribution based on a hypergeometric power series:

$$\alpha(m) = \sum_{x=m}^{\infty} \frac{(\gamma\theta/\mu) \binom{\gamma/\mu + x}{x} \binom{\theta + x}{x} (\mu/\lambda)^{x+1}}{F(\theta, \gamma/\mu, 1, \mu/\lambda) - 1}. \quad (31)$$

Here $F(\cdot, \cdot, \cdot, \cdot)$ is the hypergeometric function (Gradshteyn and Ryzhik, 1965, p. 1039). This probability distribution is a truncated, translated version of a generalized hypergeometric distribution given by Kemp (1971).

4. DISTRIBUTIONS AND EXTINCTION PROBABILITIES

The negative binomial in (29), the Poisson in (28), and the generalized hypergeometric in (31) are all weighted versions of the geometric distribution in (27). A generalized weighted distribution (Patil and Rao, 1978) takes the form

$$f^w(x) = w(x)f(x)/E[w(X)], \quad (32)$$

where $f(x)$ is a probability density, and $w(x)$ represents the weight associated with each value. Here $f(x)$ is the geometric distribution in (27), $w(x) = (1/\epsilon)^x/x!$ in (28), $w(x) = (\theta + 1)(\theta + 2) \cdots (\theta + x)/x!$ in (29), and

$$w(x) = (\theta + 1)(\theta + 2) \cdots (\theta + x)(\gamma/\mu + 1)(\gamma/\mu + 2) \cdots (\gamma/\mu + x)/(x!)^2$$

in (31). The latter two weight functions are increasing in x , giving to their corresponding probability densities heavier tails than the geometric, and hence, higher extinction probabilities for all values of m . By contrast, the extinction probability (28) is much smaller than (27) for high m values due to the unrealistically high birth rate (13).

In other applications of stochastic birth-death processes, many traditional probability distributions may emerge as forms for $\Pr[X = x]$ in (25) provided the birth and death rates are suitably chosen. For instance, the recursion relationship for such a distribution is given by

$$\Pr[X = x]/\Pr[X = x - 1] = \mu(x)/\lambda(x). \quad (33)$$

Also, $\rho(x)$ (24) frequently takes the form $\rho(x) = h(x)r^x$,

where r is a constant, and $h(0) = 1$. The probability of extinction is then the tail of a power series distribution (Patil, 1962; Ord, 1972):

$$\Pr[X = x] = h(x)r^x / \sum_{x=0}^{\infty} h(x)r^x, \quad x = 0, 1, 2, \dots \quad (34)$$

Examples seen in this paper have all been power series. An additional, unrelated example yielding the log series can be catalogued: let $\lambda(n) = \lambda \cdot (n + 1)$, $n = 1, 2, \dots$; $\lambda(0) = 0$; and $\mu(n) = \mu n$; then

$$\alpha(m) = \sum_{x=m}^{\infty} -(\mu/\lambda)^{x+1} / [(x+1)\log(1 - \mu/\lambda)]. \quad (35)$$

Finally, it is worthwhile to note a relationship between the generating functions for $\alpha(m)$ and $\Pr[X = x]$. Define the following:

$$\tau(s) = \sum_{x=0}^{\infty} s^x \Pr[X = x]; \quad \phi(s) = \sum_{x=0}^{\infty} s^x \alpha(x) \quad (36)$$

One obtains $\phi(s)$ from the familiar recursion relation for $\alpha(m)$ (see Karlin and Taylor, 1975, p. 140).

$$\alpha(m) = \alpha(m+1)\lambda(m)/[\lambda(m) + \mu(m)] + \alpha(m-1)\mu(m)/[\lambda(m) + \mu(m)], \quad (37)$$

using the conventions $\alpha(0) = 1$ and $\alpha(m) = 0$, $m < 0$. One might then utilize the relation (see Feller, 1968, p. 265)

$$\phi(s) = [1 - s\tau(s)]/(1 - s). \quad (38)$$

REFERENCES

- Abramowitz, M. and Stegun, I. A., eds. (1965). *Handbook of Mathematical Functions*. Dover, New York.
- Allee, W. C. (1938). *The Social Life of Animals*. W. W. Norton, New York.
- Andrewartha, H. G. and Birch, L. C. (1954). *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.
- Bartlett, M. S. (1978). *An Introduction to Stochastic Processes with Special Reference to Methods and Applications* (third edition). Cambridge University Press, Cambridge.

- Boswell, M. T., Ord, J. K., and Patil, G. P. (1979). Chance mechanisms underlying univariate distributions. In *Statistical Distributions in Ecological Work*, J. K. Ord, G. P. Patil, and C. Taillie, eds. International Co-operative Publishing House, Fairland, Maryland.
- Braunhaver, A. H., Graham, A. J., Bitter, B. A., Hopkins, D. E., New, W. D., Dudley, F. H., and Bushland, R. C. (1955). Screwworm control through release of sterilized flies. *Journal of Economic Entomology*, 48, 462-466.
- Costello, W. G., and Taylor, H. M. (1975). Mathematical models of the sterile male technique of insect pest control. In *Mathematical Analysis of Decision Problems in Ecology*, A. Charnes and W. R. Lynn, eds. Springer-Verlag, Berlin.
- Crowell, K. L. (1973). Experimental zoogeography: introduction of mice to small islands. *American Naturalist*, 107, 535-558.
- Feller, W. (1966). *An Introduction to Probability Theory and Its Applications, Vol. 2*. Wiley, New York.
- Feller, W. (1968). *An Introduction to Probability Theory and Its Applications, Vol. 1*. (third edition). Wiley, New York.
- Gradshteyn, I. S. and Ryzhik, I. M. (1965). *Table of Integrals, Series, and Products*. Academic Press, New York.
- Karlin, S. and Taylor, H. M. (1975). *A First Course in Stochastic Processes* (second edition). Academic Press, New York.
- Kemp, C. D. (1971). Properties of some discrete ecological distributions. In *Statistical Ecology, Volume 1*, G. P. Patil, E. C. Pielou, and W. E. Waters, eds. The Pennsylvania State University Press, University Park, Pennsylvania.
- Knippling, E. F. (1955). Possibilities of insect control or eradication through the use of sexually sterile males. *Journal of Economic Entomology*, 48, 459-462.
- Kostitzin, V. A. (1940). Sur la loi logistique et sus generalisations. *Acta Biotheoretica*, 5, 155-159.
- MacArthur, R. H. and Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Mosimann, J. E. (1958). The evolutionary significance of rare matings in animal populations. *Evolution*, 12, 246-261.
- Ord, J. K. (1972). *Families of Frequency Distributions*. Griffin, New York.
- Patil, G. P. (1962). Certain properties of the generalized power series distributions. *Annals of the Institute of Statistical Mathematics*, 14, 179-182.
- Patil, G. P. and Rao, C. R. (1978). Weighted distributions and size-biased sampling with applications to wildlife populations and human families. *Biometrics*, 34, 179-189.
- Patil, G. P. and Stiteler, W. M. (1974). Concepts of aggregation and their quantification: a critical review with some new results and applications. *Researches on Population Ecology*, 15, 238-254.

- Philip, J. R. (1957). Sociality and sparse populations. *Ecology*, 38, 107-111.
- Prout, T. (1978). The joint effects of the release of sterile males and immigration of fertilized females on a density regulated population. *Theoretical Population Biology*, 13, 40-71.
- Rade, L. (1972). On the use of generating functions and Laplace transforms in applied probability theory. *International Journal of Mathematical Education in Science and Technology*, 3, 25-33.
- Richerson, J. V., Brown, E. A., and Cameron, E. A. (1976). Premating sexual activity of gypsy moth males in small plot field tests (*Lymanthria (=Porthetria) dispar*: Lymantriidae). *Canadian Entomologist*, 108, 439-448.
- Sower, L. L. and Whitmer, G. P. (1977). Population growth and mating success of Indian meal moths and almond moths in the presence of synthetic sex pheromone. *Environmental Entomology*, 6, 17-20.
- Steiner, L. F., Hart, W. C., Harris, E. J., Cunningham, R. T., Ohinata, K., and Kamakahi, D. C. (1970). Eradication of the oriental fruit fly from the Mariana Islands by the methods of male annihilation and sterile insect release. *Journal of Economic Entomology*, 63, 131-135.
- Volterra, V. (1938). Population growth, equilibria, and extinction under specified breeding conditions: a development and extension of the logistic curve. *Human Biology*, 3, 1-11.
- Williams, G. C. (1975). *Sex and Evolution*. Princeton University Press, Princeton, New Jersey.

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