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1974 PROGRESS REPORT

**USE OF THE NORMAL GENERATING DISTRIBUTION FOR
ESTIMATING POPULATION SURVIVAL**

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**US/IBP DESERT BIOME
RESEARCH MEMORANDUM 75-51**

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$$\hat{\xi} = \sum_{i=1}^n \Phi^{-1}(s_i)/n \quad (11)$$

$$\hat{\tau}^2 = \sum_{i=1}^n (\Phi^{-1}(s_i) - \hat{\xi})^2/n \quad (12)$$

A check for bias in these estimators shows that $\hat{\xi}$ is unbiased while $\hat{\tau}^2$ can be made unbiased by multiplying Equation 12 by the quantity $n/(n-1)$.

HYPOTHESIS TESTING CONCERNING *n.g.d.* $q(s)$

In certain instances it may be required to test hypotheses concerning $q(s)$. For example, to test $H_0: q(s) = q'(s)$, where $q'(s)$ is a specified form of $q(s)$, against an appropriate alternative, amounts to testing $H_0: \xi = \xi'$ and $H_0: \tau^2 = \tau'^2$ against the chosen alternatives. Such tests can be performed by observing that $\hat{\xi}$ given by Equation 11 is normally distributed while $(n-1)\hat{\tau}^2/\tau^2$ is chi-square distributed with $n-1$ *d.f.* The estimate $\hat{\tau}^2$ is calculated from Equation 12 and corrected for bias. The observations s_1, s_2, \dots, s_n must, of course, be independent for these distributions to hold.

The distributions of $\hat{\xi}$ and $\hat{\tau}^2$ follow from Equation 5 which can be written:

$$\mu_x = \sigma_x \Phi^{-1}(s) \quad (13)$$

Since μ_x is by definition normally distributed, Equation 13 implies the same for $\Phi^{-1}(s)$. Therefore, from Equations 11 and 12, $\hat{\xi}$ and the unbiased form of $\hat{\tau}^2$ are normally and chi-square distributed, respectively.

MODEL PARAMETER DEPENDENCE

Measures of mean survival and the probability of survival less than a specified level s^* are of interest to population control. The dependence of each upon the model parameters μ_1 , σ_1 and σ_x is examined in the following.

Using $\xi = (\mu_1/\sigma_x)$ and $\tau^2 = (\sigma_1/\sigma_x)^2$, the mean survival $E(s)$ given by Equation 9 can be reformulated as

$$E(s) = \Phi [\mu_1/\sqrt{(\sigma_x^2 + \sigma_1^2)}] \quad (14)$$

It follows from the sigmoid relation $\Phi(\cdot)$ that, for a given σ_x^2 and σ_1^2 , $E(s)$ increases with mean extensity μ_1 , the greatest rate of increase occurring where $\mu_1 = 0.0$. Conversely, holding μ_1 constant and varying σ_x^2 or σ_1^2 changes $E(s)$ according to the value assumed by μ_1 . If $\mu_1 < 0$, $E(s)$ increases with increasing σ_x^2 or σ_1^2 ; if $\mu_1 = 0$, $E(s)$ does not change with σ_x^2 or σ_1^2 ; if $\mu_1 > 0$, $E(s)$ decreases with increasing σ_x^2 or σ_1^2 .

A second measure is the probability a realized value for survival less than a specified level s^* occurs. The concern is that a low value of s in a given year reduces the population size to a point where its resource value vanishes or, at the extreme, becomes nonsustaining. The condition imposed is

$$Q(s^*) = \Phi [(1/\tau)(\Phi^{-1}(s^*) - \xi)] < p \quad (15)$$

where $Q(s^*)$, as given by Equation 8, is restricted to being less than a specified value p . The objective is to determine the parameter space satisfying Equation 15. With some algebra this translates to:

$$\Phi^{-1}(s^*) \sigma_x - \Phi^{-1}(p) \sigma_1 \leq \mu_1 \quad (16)$$

Of general interest to extinction are small values of s^* and p such that $s^*, p < 0.5$. This implies $\Phi^{-1}(s^*), \Phi^{-1}(p) < 0$. With this understanding, if Equation 16 is satisfied for any set of values σ_x , σ_1 , μ_1 , it will remain satisfied if σ_x and/or μ_1 are made arbitrarily large or σ_1 is reduced to zero.

Habitat manipulation which raises the mean strength μ_v by making food more abundant, or decreases the mean stress μ_u by creating an improved shelter complex, leads to increased mean extensity μ_1 . From the above it follows that increasing μ_1 increases the mean survival $E(s)$ and reduces the probability of extinction $Q(s^*)$. Habitat control, however, would likely alter σ_x^2 , and it is conceivable, although unconfirmed, that manipulation might raise μ_1 but alter σ_x^2 so that survival s actually decreases. Ideally, the strategy for a maximal increase in $E(s)$, in addition to increasing μ_1 , is to increase σ_x^2 if $\mu_1 < 0$ and decrease σ_x^2 if $\mu_1 > 0$. Whether μ_1 is positive or negative can be decided by estimating ξ from data using Equation 11 and testing $H_0: \xi = 0$ against the appropriate alternative.

It does not follow, however, that increased mean survival $E(s)$ implies a reduced probability of extinction. If $\mu_1 > 0$ and σ_x^2 is decreased, then $E(s)$ will increase but $Q(s^*)$ will also increase. This can be explained by reference to Figure 1, curves 7 and 9. If $\mu_1 > 0$, then $\xi > 0$, and if $\tau^2 < 1$, then decreasing σ_x^2 will at some point cause $\tau^2 > 1$. This process results in an increase not only in $E(s)$ but in $Var(s)$ as well, and an increase in the probability contained in the lower tail of the $q(s)$ curve.

Equation 16 makes explicit the relationship between climatic variation among years and variation in extensity exhibited by the organism in its environment, σ_1^2 and σ_x^2 respectively. The two are opposed; when great variation in climatic stress exists among years (σ_1^2 large), the probability of extinction is minimized by making σ_x^2 as large as possible by habitat manipulation. Also, the organisms' behavior may be relevant in changing σ_x^2 through the dependence of σ_x^2 upon the strength-stress correlation ρ (Equation 3). If strong animals occupy low-stress microhabitats and weak animals occupy a high-stress area, $\rho < 0$ and σ_x^2 is increased compared to that for random habitat occupancy. It follows that the optimal behavioral strategy to minimize extinction over the stress period is for nature to prescribe $\rho < 0$.

CONSEQUENCES OF NONNORMALITY

The assumption of normality appears in Axiom 5 where extensity μ_x is taken as normally distributed as $g(\mu_x)$. The transforming function, of general form $s = h(\mu_x)$, is the cumulative normal distribution given by Equation 5. The

sigmoid curve $s = h(\mu_x)$, in Figure 2 is purposely skewed to represent a nonnormally distributed extensity, and $g(\mu_x)$ is also skewed. The transformation (Equation 6) can be evaluated graphically by drawing $q(s)$ so that any bounded area under the $q(s)$ curve equals the corresponding area under the $g(\mu_x)$ curve, as indicated by the shading in Figure 2. Under conditions where μ_1 is varied and where $s = h(\mu_x)$ remains sigmoid and $g(\mu_x)$ bell-shaped, although both are quite skewed, the transformed curve can be adequately fit by $q(s)$ (Equation 1); the resulting shapes are well characterized by those shown in Figure 1. Thus, exact normality is not important. However, severe nonnormality which departs from being bell-shaped, such as multimodal distributions, yields striking cases which are ill fit by the *n.g.d.* $q(s)$.

EXAMPLES OF ESTIMATED $q(s)$ CURVES

Figure 1 gives typical $q(s)$ curves for a partition of the ξ and τ^2 parameter space. In practice, $\hat{\xi}$ and $\hat{\tau}^2$ can be calculated from the observations s_1, s_2, \dots, s_n using Equations 11 and 12 and Figure 1, used to identify the general form of the survival density. The specific form can be obtained from Equation 1 and probability statements concerning survival from Equation 8.

Nine sets of population survival data taken from the literature were used to generate $q(s)$ curves: 1) grouse brood survival, Connecticut Hill study area (Darrow 1947a, p. 315); 2) grouse brood survival, Adirondack study area (Darrow 1947a, p. 315); 3) adult grouse over-winter survival, Connecticut Hill study area (Darrow 1947b, p. 531); 4) adult grouse over-winter survival, Adirondack study area (Darrow 1947b, p. 531); 5) juvenile partridge over-winter survival (Severtzoff 1934, p. 419); 6) great tit summer-to-spring survival (Lack 1968, pp. 60-61); 7) bobwhite over-winter survival (Errington 1945, p. 13); 8) bobwhite over-winter survival (Kozicky and Hendrickson 1952, p. 484); 9) yearly survival of young roe deer (Severtzoff 1934, p. 422). Page references give location of tabular data as shown in Figure 3 and Table 1; none is bimodal as in curves 3, 6 and 9 in Figure 1. Bimodal curves result when the variance of μ_x among years exceeds the variance of the extensity, that is $(\sigma_1/\sigma_x)^2 = \tau^2 > 1$. Referring to the graphical transformation (Figure 2) for given μ_1 and σ_x^2 , the larger σ_1^2 becomes, the greater is the spread of realizations of μ_x along the abscissa and hence the

probability of s being near 0 or 1 increases. The effect is most conspicuous when the mean of $g(\mu_x)$, or μ_1 , is zero, so that $q(s)$ is symmetric. If $\tau^2 = 1$, $q(s)$ is the uniform distribution; if $\tau^2 < 1$, $q(s)$ is unimodal with mode at $s = 0.5$; if $\tau^2 > 1$, there are modes at $s = 0$ and 1 and an antimode at $s = 0.5$ (Figure 1, cases 5, 4, 6).

Thus, as σ_1^2 becomes larger than σ_x^2 , $q(s)$ becomes bimodal and there is an increase in the probability of low (and high) survival. Hence bimodal forms may be rare or nonexistent in nature. This behavior can also explain the end of range for a population of animals or plants. For example, the terminus of a forest occurs where σ_1^2 begins to exceed σ_x^2 even though μ_1 remains constant as the boundary is approached.

SUMMARY

Given a set of independent survival data s_1, s_2, \dots, s_n for a given population obtained over n years, the normal generated distribution (*n.g.d.*; Equation 1) developed by Chiu (1974) can be used to obtain the distribution of survival proportions. Maximum likelihood estimates of the parameters ξ and τ^2 can be found from Equations 11 and 12 and the cumulative distribution function $Q(s)$ (Equation 8) used to give probability estimates of survival. Hypothesis tests concerning the distribution of survival can be performed based upon the distributions of the parameter estimates $\hat{\xi}$ and $\hat{\tau}^2$.

The axioms leading to the *n.g.d.* depend upon assumptions of normality regarding the abstract concept of extensity. These cannot be subjected to empirical study. However, the model is robust for departures from normality that retain the bell-shaped feature. In any application, the researcher has knowledge of the survival process beyond the observations s_1, s_2, \dots, s_n . Comparison of this knowledge with probability statements derived from the model is the most practical way to judge model validity.

The relationships among the parameters μ_1, σ_1^2 and σ_x^2 concisely describe how man- or self-regulating controls affect survival. These relationships hold in an idealized setting given by the model axioms. Still, they raise useful questions regarding the concepts of habitat management and population self-regulation strategies.

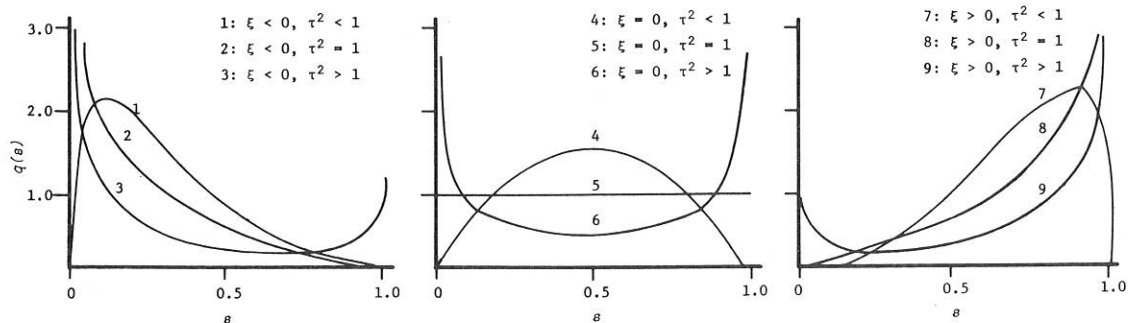


Figure 1. Typical probability densities of survival proportions, $q(s)$ by the normal generated distribution (Equation 1) for parameter space ranges: $\xi <, =, > 0$; $\tau^2 <, =, > 1$.

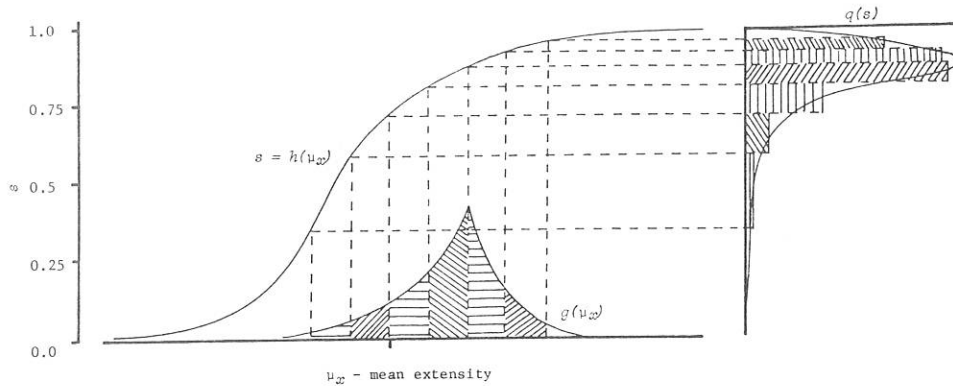


Figure 2. Graphical method for transforming $g(\mu_x)$ using $s = h(\mu_x)$ to obtain $q(s)$. The transformation preserves corresponding shaded areas under the $g(\mu_x)$ and $q(s)$ curves. $g(\mu_x)$ and $s = h(\mu_x)$ are not normal, but $q(s)$ is still approximately *n.g.d.* distributed.

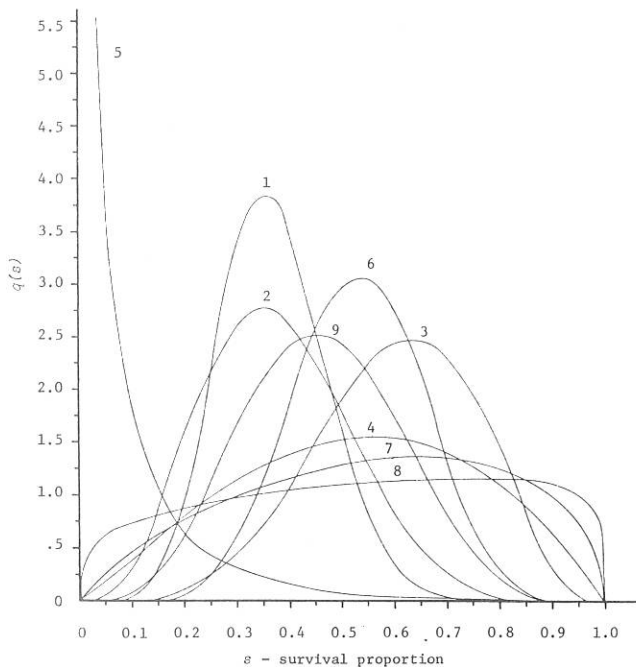


Figure 3. Normal generated distribution $q(s)$ fitted to survival realization s_1, s_2, \dots, s_n taken from the literature. Case numbers identify curves; references to data used are given in text.

Table 1. Estimated parameters $\hat{\xi}$ and $\hat{\tau}^2$, mean $E(s)$ and standard deviation S.D. (s) and number of observations n for $q(s)$ curves given in Figure 3

Case	$\hat{\xi}$	$\hat{\tau}^2$	$E(s)$	S.D. (s)	n
1	-.351	.0772	.368	.101	13
2	-.335	.150	.377	.138	11
3	.277	.177	.601	.151	12
4	.0858	.417	.529	.218	7
5	-2.03	.805	.0656	.107	23
6	.081	.106	.531	.123	11
7	.159	.565	.551	.241	15
8	.131	.799	.539	.270	11
9	-.103	.158	.462	.147	12

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