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THE MINIMUM VIABLE POPULATION PROBLEM
I. THE DEMOGRAPHY OF CHANCE EXTINCTION
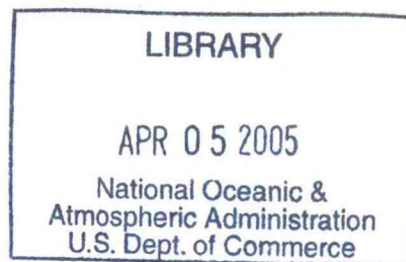
By

Daniel Goodman

ADMINISTRATIVE REPORT LJ-84-44C

THE MINIMUM VIABLE POPULATION PROBLEM

I. THE DEMOGRAPHY OF CHANCE EXTINCTION

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ABSTRACT

A generalized birth and death process serves as a simple, flexible model for computing the expected persistence time of a small population in a random world. We may reparametrize the model in ways that allow explicit incorporation of density depedendence, random differences between events experienced by individuals, and random environmental variation. We find that environmental variation poses a greater problem for population persistence than does individual variation, and that, comparatively, details of the form of the growth curve are not especially important, as long as the expected growth rate is positive. In particular, we find that with purely individual variation, the expected persistence time increases approximately with the power of the ceiling on population size; but with purely environmental variation, the expected persistence time increases approximately linearly with the size of the population ceiling. We discuss some aspects of reserve design and management in light of these results, noting in passing that an idealized system of separate reserves managed according to a reintroduction policy will confer a longer persistence time than a single reserve with the same total carrying capacity, but in the absence of the reintroduction policy the system of smaller separate reserves confers a shorter persistence time than the single large reserve.

ACKNOWLEDGEMENTS

INTRODUCTION

With many sorts of habitats, and indeed some entire ecosystems, dwindling in extent, the extinctions of many species are imminent. Attempts at saving some of these species as ecologically functioning members of more or less natural communities, rather than zoo populations, involve the establishment of reserves whose extent is very modest in comparison to the original range of the species, and which, for that reason, can only maintain comparatively small relict populations. We are concerned, therefore, to estimate the viabilities of these small populations, and to learn what management measures and reserve-design features will enhance their viabilities. Furthermore, since there is inevitably pressure, in a crowded world, to encroach upon reserves, we should like to estimate the extent of minimum reserve that will suffice to confer upon a population an expected time of extinction that is, by some criterion, acceptably remote. We shall scale this measure of reserve extent in units of population size. This is the minimum viable population problem.

At the most elementary level, the minimum viable population problem can be framed in demographic terms; but the magnitudes of the demographic variables will depend on a variety of factors, such as habitat quality, environmental variation, and genetic composition of the population (Schaffer, 1981; Soule, 1980).

In this paper, we will, with a simple model, examine the relation between the expected survival time of a population and its associated demographic variables, the values of which are

determined by the life history and by environmental statistics. In the discussion, we will relate the results of these analyses of properties of population models to considerations of population management, habitat management, and reserve design.

Subsequent papers in this series will treat the matter of adaptive evolution in small populations and the problem of reduced fitness owing to inbreeding. Briefly anticipating the results of these analyses, some of which build on the methods developed in the present paper, we will find we are summarily pessimistic about the possibility of continued evolution in relict populations, but we can be guardedly optimistic about the management of inbreeding depression.

CHANCE EXTINCTION

Self evidently, a population goes extinct when its last member dies. This death may be due to various causes, and among those causes will be many where "chance" plays a role. Similarly, the population is reduced to its last member when its second to last member dies, and this death too may be due to chance, etc. In this perspective then, we might conclude that, aside from extremely thorough catastrophes, populations become extinct, at least proximately, because of bad luck.

Ultimately, of course, we would want to inquire into the circumstances that exposed the population to this luck. If we were compiling an evolutionary narrative, we would doubtless call these circumstances the "cause" of the extinction. Yet it is informative to pursue the idea that luck dealt the final blow, for this motivates a search for the mathematical connection between what we

are loosely calling the "circumstances" of the population and the "life expectancy" of that population in a somewhat unpredictable world.

If we were concerned with a particular population, about which much was known, we might construct a detailed model relating the dynamics of reproduction, maturation and mortality to environmental variables; and then we could set a computer to sampling environmental states and demographic events according to distributions which we had already decided were realistic. In this manner, we could, in successive trials, generate a distribution of the times to extinction under the model, and arrive at summary statistics applicable to that population under the given circumstances. This approach is illustrated by Shaffer's (1983) analysis of the dynamics of a small population of grizzly bears.

For a more general picture of the determinants of expectable persistence time, we must necessarily paint with a much broader brush, reducing the dimensionality of the determinants to the barest minimum, so that the underlying relationships can be discernible. We will adopt this minimalist strategy for the present analysis.

A BIRTH AND DEATH PROCESS

The simplest flexible mathematical representation of a finite population which may increase, by one birth at a time, or decrease, by one death at a time, with a random element in these increases and decreases, is the continuous time Markov chain called, appropriately enough, a birth and death process. At the heart of the random element in this model is the stipulation that

births and deaths occur in a manner like that of radioactive decay: birth and death events are described merely as having probabilities of occurrence (per individual), and these probabilities are not directly affected in any way by the past history of the individual, except obviously that a death event terminates the history of that individual.

Under the birth and death model, for any individual in the population, the probability of death during a short time interval Δt is given as as $u \Delta t$, (more precisely as $u \Delta t + o(\Delta t)$, but since we have stipulated a short interval we ignore the $o(\Delta t)$ term) where u is referred to as the death rate, which is not explicitly time or age dependent. Thus for a situation where u remains constant, the probabability that an individual, alive at time 0, will still be alive at time t is $\exp(-ut)$. Put another way: for any individual in the population, the remaining time until death is an exponentially distributed random variable with parameter u, so that the mean time remaining is $1/u$, and the variance in the time remaining is $1/u^{**}2$.

Similarly, for any individual in the population, the probability of giving birth (to one more individual) during a short time interval Δt is given as $b \Delta t$ (again this is actually $b \Delta t + o(\Delta t)$, as above), where b is referred to as the birth rate, which is not explicitly time or age dependent. Thus for a situation where b remains constant, the probability that an individual, observed at time 0 and still alive at time t, will not yet have given rise to a birth in this interval is $\exp(-bt)$. Put another way: for any individual observed in the population, the

time until it next gives birth (unless death intervenes) is an exponentially distributed random variable with parameter b, so that the mean of the time till the next birth (for a surviving individual) is 1/b, and the variance is 1/b**2.

Finally, birth and death events, in this model, are treated as independent, and the events in each individual are treated as independent.

It is clear, from this description, that some aspects of the "randomness" in the demography of real populations are captured in a very natural way by the "birth and death process," whereas other aspects seem rather remote from the premises of model. We will need to be very careful about our understanding of the assumptions of the model in order to tailor it to our actual applications.

Despite the premonition that we may have to pound some square pegs into round holes in using the birth and death process as a model for the dynamics of reserve populations, we can see the attraction of this model: Superficially, it seems to be determined by only two parameters, the birth rate and the death rate, resulting in a parameter space that we can readily explore in a very thorough way. In general, there will actually be different values of the parameters for every possible number of individuals that can comprise the population, but we can still keep the parameter space quite simple by considering a few general types of "density dependence" for the birth rate and death rate parameters.

The birth and death process was first developed by Feller (1939). The behavior of simple versions of this model, where no bound is placed on the population size, and where the per capita

rates, u and b, are constant, have been investigated at some length (Feller, 1939). In particular, it is known that the expected value of the population size, at time t, starting with a population of one at time zero, is

$$E\{n(t)\} = e^{(b-u)t} \tag{1}$$

recapitulating the familiar exponential growth form of the determininstic process. The variance in the size of this population at time t is

$$Var\{n(t)\} = \frac{(b+u)}{(b-u)} * e^{(b-u)t} (e^{(b-u)t} - 1) \tag{2}$$

In these models, with no limit on the population size, a population initiated at size n(o) has some probability of indefinitely escaping extinction by growing indefinitely numerous, provided its expectation of growth is positive. The probability of such an "escape" in a model with constant per capita rates is (Kendall, 1949)

$$1-Po(t) = 1 - (u/b)^{n(o)} \qquad t \to \infty \tag{3}$$

Kendall (1948) observed that the parameters u and b could be made functions of time, and could be adjusted to achieve any stipulated trajectory for the expectation of the population size. Bartlett (1960) showed that making the values of u and b specific to each population size could achieve dynamics whose expectations recapitulate familiar density dependent models of deterministic population growth.

MacArthur (1972) considered the case where there is a fixed

population ceiling, k, with b and u constant, showing, for example, that the expected time to extinction of a population intiated with 1 individual is

$$t(1) = \frac{1}{b} \sum_{j=1}^{k} \frac{1}{j} \left(\frac{b}{u}\right)^{**}j$$

$$\sim \frac{1}{bk} \left(\frac{b}{u}\right)^{**}k \qquad [4]$$

Slightly rearranging the algebra, we find that the expected time to extinction, in MacArthur's model, of a population initiated at its ceiling k is

$$t(k) = \left(\frac{1}{b-u}\right) \sum_{j=1}^{k} \frac{1}{j} \left[\left(\frac{b}{u}\right)^{**}j -1\right]$$

$$\sim \frac{1}{k(b-u)} \left[\left(\frac{b}{u}\right)^{**}k -1\right] \qquad [5]$$

We shall next extend MacArthur's model to encompass a situation where the birth rate and death rate are not fixed, and then we shall reexpress the model in terms of parameters that are more natural for the problem under consideration.

PERSISTENCE TIME IN THE GENERAL BIRTH AND DEATH PROCESS

Consider a population, governed by a birth and death process, where the birth rates and death rates are arbitrary functions of the population size, so for a population of size n, we denote the per capita birth rate as b(n), and the per capita death rate as

$u(n)$. Denote the expected time to extinction for a population of size n at time zero as $t(n)$.

Following the argument explained by MacArthur (1972), we note the relationship between $t(n)$, $t(n-1)$ and $t(n+1)$. The expected persistence time of a population of size n, must be equal to the mean time for that population's first change, which may be either an increase by one or a decrease by one, plus the persistence times of the resulting larger or smaller populations weighted by the respective probabilities that the next change is an increase or a decrease:

$$t_{(n)} = \frac{1}{(b_{(n)}+u_{(n)})\,n} + \left(\frac{b_{(n)}}{b_{(n)}+u_{(n)}}\right) t_{(n+1)} + \left(\frac{u_{(n)}}{b_{(n)}+u_{(n)}}\right) t_{(n-1)} \qquad [6]$$

Let the population have a ceiling of k, so that $b(k)=0$. Given also, obviously, that $t(0)=0$, we thus have a system of k equations of the above form, where the k values of $b(n)$ and the k values of $u(n)$ constitute knowns, and the k values of $t(n)$ constitute unknowns.

Each of the k equations of the above form may be rearranged to

$$1 = a_{(j,j-1)}\, t_{(j-1)} + a_{(j,j)}\, t_{(j)} + a_{(j,j+1)}\, t_{(j+1)} \qquad [7]$$

where

$$a_{(j,j)} = (b_{(j)}+u_{(j)})\, j \qquad [8]$$

$$a_{(j,j+1)} = -b_{(j)}\, j \qquad [9]$$

$$a_{(j,j-1)} = -u_{(j)}\, j \qquad [10]$$

We have k such equations, one for each integer value of j from 1 to k, where, for the equation with j=1 we need not bother

with the a(1,0) term because t(0)=0, and for the equation with j=k
we need not bother with the a(k,k+1) term since b(k)=0.

The motivation for the double subscripting is to re-express
the set of k equations in matrix notation

$$\underline{1} = A\underline{t} \qquad\qquad [11]$$

where $\underline{1}$ is the vector of ones, $\underline{t}$ is the vector of expected
extinction times for populations initialized at the various
densities 1 through k, and A is the tridiagonal matrix, whose
elements a(i,j) are as given above for j=i j=i+1 and j=i-1, and
the remainder of whose elements are zero. Thus we have a ready
solution for the expected times to extinction:

$$\underline{t} = A^{-1} * \underline{1} \qquad\qquad [12]$$

so that

$$t(j) = \sum_{i=1}^{k} c(j,i) \qquad\qquad [13]$$

where the c's are elements of the matrix A inverse. The
computational effort in inverting A is substantially reduced by
capitalizing on the tridiagonal form.

REPARAMETRIZATION OF THE BIRTH AND DEATH PROCESS

The birth and death rate parameters of the birth and death
process are not exactly isomorphic to the demographic parameters,
mean per capita birth rate and mean per capita death rate, in a
real population. In the birth and death process model, the birth
and death rate parameters play two roles, in that they determine
both the expected growth rate of the population and the variance
of the growth process.

In their role in determining the expected growth rate, in the birth and death process, the birth and death rate parameters act in a way which is familiar from the deterministic demographic model, with the expected growth rate being (b-u), as will be developed below. In their role in determining the variance of the growth process, the two parameters act in a way that is peculiar to the birth and death process model, and which, from the standpoint of our interest in real populations, may be construed as substantially artificial. For this reason, we will reparametrize the model in terms of the expected growth rate and a measure of the variance in the growth rate, so that we can stipulate values for growth rate and variance to suit our application. Then we will simply calculate the values of b and u which give the desired growth rate and variance in a birth and death process model, and we will plug these values into the algebra of the previous section in order to solve for the expected time to extinction.

a. The expected growth rate

Consider a time increment, Δt, which is so short that the population growth, in absolute terms, during this interval is negligible. Then, if we think of the "parent" population as constant during this interval, the births and deaths which accrue to this parent population during the interval may be represented as two simple, independent exponential processes, with parameters b(n)n and u(n)n respectively, where n is the size of the population. Accordingly, the numbers of births, and deaths, respectively, in the time interval Δt, are independent Poisson

distributed variables, with expectation $b(n)n \Delta t$ and $u(n)n \Delta t$ respectively.

During the interval Δt, the net population change, Δn, is the difference between accrued births and accrued deaths, the expectation of which is simply the difference between the expectations of the two independent Poisson variables.

$$E[\Delta n] = [b(n)-u(n)] \, n \, \Delta t \qquad [14]$$

Define the expected instantaneous growth rate of the population as

$$E(r) = E \left\{ \frac{1}{n} \frac{dn}{dt} \right\} = \frac{1}{n} \lim_{\Delta t \to o} \left\{ \frac{E[\Delta n]}{\Delta t} \right\}$$

$$= b(n)-u(n) \qquad [15]$$

b. A measure of variance in the growth rate

Define the variance in the growth rate as the variance in the quantity

$$r = \frac{1}{n} \lim_{\Delta t \to o} \left\{ \frac{\Delta n}{\Delta t} \right\} \qquad [16]$$

where Δn is the difference in two independent Poisson variables.

Since, for a Poisson variable the variance is equal to the mean, and for two independent random variables the variance of their difference is the sum of their two respective variances, we have

$$Var(r) = \frac{1}{n^{**}2} \, Var(\lim_{\hat{} t \to o} \left\{ \frac{\Delta n}{\Delta t} \right\})$$

$$= \frac{b(n)+u(n)}{n} \qquad [17]$$

Accordingly, for a stipulated mean growth rate, $E[r(n)]$, associated with a stipulated variance in growth rate, $Var[r(n)]$, as defined above, at a given population size n, the required values of the parameters for the birth and death process are:

$$u(n) = \frac{n\ Var[r(n)] - E[r(n)]}{2} \qquad [18]$$

and

$$b(n) = E[r(n)] + \frac{n\ Var[r(n)] - E[r(n)]}{2}$$

$$= E[r(n)] + u(n) \qquad [19]$$

completing the parametrization.

c. The meaning of the variance in the model

For a real population, there are two essential components of variance in the growth process. One of these components operates independently in each individual. Examples of such variation would be the chance element of sex at birth, or the way in which each individual "samples" the universe of "accidental" death or chance opportunities for reproduction. The second component operates on the entire population. Examples of this kind of variation would be population-wide changes in the probabilities of death or reproduction owing to "environmental" events such as weather changes, or vagaries of disease, competition, predation and resource availability. For convenience we will label these two components of variance "individual" and "environmental."

The birth and death process model represents the variance as "individual" variance only. With the constant per capita rates, therefore, the variance, becomes very small as the population

increases, since the individual variation is being averaged over a larger and larger sample of individuals. That is, for b and u independent of population size, the variance is inversely proportional to the population size, as is seen in equation (17) with b(n)=b and u(n)=u.

In order to incorporate some variation in the spirit of "environmental" variance in the birth and death process model we use, we must force u(n) and b(n) to get larger and larger, with n, all the while preserving a difference between b(n) and u(n) that satisfies our stipulated value for the growth rate r(n).

Note that in its essence, "environmental" variance, within the "same" environment, will be independent of the population size. Thus we can actually parametrize in terms of the two variance components: we may stipulate a value for the individual component of variance (i.e., the differences between individuals) expressed as V1, the variance owing to these differences alone in a hypothetical population of one individual, and we may stipulate a value for V(env) the density independent variance owing to environmental variations. Then provided we believe that the per capita variation owing to the "individual" component is constant with density, the total variance, at any density n, is

$$Var[r(n)] = \frac{V1}{n} + V(env) \qquad [20]$$

If the per capita variation owing to the individual component is itself a function of density, as might be reasonable where there is gradual density dependence of the demographic mortality rates and birth rates, we would have

$$\text{Var}[r(n)] = \frac{V1(n)}{n} + V(env) \qquad\qquad [21]$$

where V1 is a function of n, as desired, for example treating V1(n) as a linear function of r(n).

In this manner, we can represent a wide variety of patterns of variation, despite the strictures of the birth and death process model. The one feature we cannot change is that the birth and death process model inevitably represents all variation as temporally "fine grained", in fact assuming zero serial correlation at all non zero lags, whereas in real populations in real environments there is substantial serial correlation owing to age structure (which is more or less a part of the "individual" component of variance) and temporal patterns in environmental variation (most notably seasonality, where there may be seasonal "bottlenecks" usually a stressful dry season or cold season, through which the population must pass). In other words, even though we can tailor the model to the desired value of variance, we must be extremely circumspect in translating our estimates from a "coarse grained" world to a parameter value in a fine grained model. In general, this will be accomplished by basing our estimate on observations during a time interval which is long enough for the coarse grained variation to be manifest, and then amortizing this variation to obtain a parameter value that essentially refers to an "instant" in the model. An example of this calculation, and an accompanying simulation which verifies the practical accuracy of the model, will be presented elsewhere.

Obviously, this collapsing of the structure of real

populations in real environments to fit the assumptions of the birth and death process must result in some innaccuracy for any particular population; but it does achieve the goal of reduced dimensionality, and it does offer indefinite flexibility in the reduced space, so as to capture the essence of the variation in the actual population, provided we exercise sufficient care in arriving at our estimates of parameter values. Given that the actual available data on variances in the demography of real populations are in any case sketchy (the sampling properties of variances, particularly with serial correlation, are not encouraging), this approach should certainly be adequate to elucidate any patterns that might be discernible within the resolution of our data.

THE RELATION BETWEEN PERSISTENCE TIME AND POPULATION SIZE FOR PURE ENVIRONMENTAL VARIANCE

MacArthur's (1972) analysis, since it treated u and b as constants, dealt with a system that, in our notation, represented the demographic variance as pure individual variance. In this system, we see from equation (5), that the expected time to extinction will increase approximately with the power of k, for k not small (as the exponential term then dominates the inverse dependence in the denominator). This is to say that the adverse effects of individual variance are readily escaped by increasing population size, which is consistent with equation (21), which shows the variance due to individual differences decreasing asymptotically to zero as the population size increases.

Since pure environmental variance does not diminish with population size in our model, we may expect that it will pose a more severe problem for population persistence.

Consider a situation where the only variance in the growth rate is pure environmental variance which we represent as a constant value v, and where the expected growth rate is also constant, which we represent as a constant value r for all population sizes less than k. Then, from equations (18) and (19)

$$u(n) = \frac{nv-r}{2} \tag{22}$$

and, for n<k

$$b(n) = \frac{nv+r}{2} \tag{23}$$

with b(k)=0 by definition.

Then the k equations of the form of equation (7), when written in terms of the u(n) and b(n), as in equations (8), (9), and (10), yield, for 0<i<k, (recall that t(0)=0)

$$1 = -i(\frac{iv-r}{2})t_{(i-1)} + i^2 vt_{(i)} - i(\frac{iv+r}{2})t_{(i+1)} \tag{24}$$

and for i=k

$$1 = -k(\frac{kv-r}{2})t_{(k-1)} + k(\frac{kv-r}{2})t_{(k)} \tag{25}$$

Equation (24) may be written as the recursion

$$(t_{(i)}-t_{(i-1)}) = \frac{2}{i(iv-r)} + (\frac{iv+r}{iv-r})(t_{(i+1)}-t_{(i)}) \tag{26}$$

which applies for i=1,2,3,...(k-1), while for i=k, from equation (25),

$$(t_{(k)}-t_{(k-1)}) = \frac{2}{k(kv-r)} \tag{27}$$

So starting with

$$t_{(1)} = (t_{(1)} - t_{(0)}) = \frac{2}{(v-r)} + (\frac{v+r}{v-r})(t_{(2)} - t_{(1)}) \qquad [28]$$

we iteratively apply equation (26) to substitute for the last difference term on the right, obtaining after (k-1) iterations an expression with $(t_{(k)} - t_{(k-1)})$ on the right, for which we may substitute equation (27) yielding finally

$$t_{(1)} = \sum_{i=1}^{k} \frac{2}{i(iv-r)} \prod_{j=1}^{i-1} (\frac{jv+r}{jv-r})$$

$$= \frac{2}{(v-r)} \sum_{i=1}^{k} \frac{1}{i} \prod_{j=1}^{i-1} (\frac{jv+r}{(j+1)v-r}) \qquad [29]$$

For r<(v/2), all the terms in the product sequence are ratios less than one, so we have immediately that t(1) must be considerably less than 2k/(v-r). The restriction on r is very mild, for even under the simple assumptions of the classic birth and death process, where births and deaths are exponential, and where there is no "environmental" variance, r is inevitably less than v by 2u for a single individual.

For small r, and other parameters in reasonable ranges, we may safely disregard r in the ratio (jv+r)/([j+1]v-r), obtaining

$$t_{(1)} \sim \frac{2}{(v-r)} \sum_{i=1}^{k} \frac{1}{i**2} \qquad [30]$$

which grows very much more slowly than linearly with k. Indeed for

k not small, this expression for t(1) will hardly grow at all with k, since the sum of the infinite series $1/i**2$ is only $\pi**2/6$, roughly 1.6. This expression for t(1) increases with r and decreases with v, as expected.

There remains only the question of relating t(k) to t(1). Consider the set of k equations consisting of (k-1) equations of the form of equation (26), with i=1,2,3,...(k-1), and equation (27). Adding together the left sides of all these equations, and the right sides, yields, after slightly rearranging the summations

$$t_{(k)} = 2\sum_{i=1}^{k}\frac{1}{i(iv-r)} + t_{(k)}\left(\frac{[k-1]v+r}{[k-1]v-r}\right) - t_{(1)}\left(\frac{v+r}{v-r}\right) + 2rv\sum_{i=2}^{k-1}\frac{t_{(i)}}{([i-1]v-r)(iv-r)}$$

[31]

Since the last summation in equation [31] is just a weighted sum of t(i)'s, with all the weights positive for r<v, and since t(i) increases monotonically with i, there must be a value $t(1) < \hat{t} < t(k)$ for which

$$\sum_{i=2}^{k-1}\frac{t_{(i)}}{([i-1]v-r)(iv-r)} = \hat{t}\sum_{i=2}^{k-1}\frac{1}{([i-1]v-r)(iv-r)}$$

[32]

On inspection, the denominator in the above summations gets large very rapidly as i increases, so $\hat{t}$ must be rather closer to t(1) than to t(k). Substituting equation (32) into (31), and rearranging

$$t_{(k)} = ([k-1]v-r)\left\{\left(\frac{v+r}{v-r}\right)\frac{t_{(1)}}{2r} - \frac{1}{r}\sum_{i=1}^{k}\frac{1}{i(iv-r)} - v\hat{t}\sum_{i=2}^{k-1}\frac{1}{([i-1]v-r)(iv-r)}\right\}$$

[33]

-19-

Since $t_{(1)}<\hat{t}$, if we substitute $t_{(1)}$ for $\hat{t}$ in equation (33) we obtain the inequality

$$t_{(k)} < ([k-1]v-r)\{(\frac{v+r}{v-r})\frac{t_{(1)}}{2r} - \frac{1}{r}\sum_{i=1}^{k}\frac{1}{i(iv-r)} - vt_{(1)}\sum_{i=2}^{k-1}\frac{1}{([i-1]v-r)(iv-r)}\} \qquad [34]$$

Approximate equation (30) showed that $t_{(1)}$ hardly grows at all with k, once k is not small. The two summations in inequality (34), similarly, for small r, behave like the summation $i/i**2$, so these too are largely unresponsive to k for k not small. Thus the entire expression in curly brackets in inequality (34) does not grow appreciably with k, once k is no longer small; so we have it, then, that the dominant role of k in the right hand side of inequality (34) is the linear expression outside the curly brackets. In other words, $t_{(k)}$ can not grow faster than, roughly, linearly with k.

Further, substituting equation (30) above, disregarding r in the summations wherever it appears in a sum or difference with some other value, replacing the summations of $1/i**2$ with their limiting value, and noting that the infinite series $1/i(i-1)$ sums to 1, we obtain the rough approximation, for small r,

$$t_{(k)} < \frac{([k-1]v-r)\pi^2}{(v-r)6v}\{\frac{3v-r}{(v-r)} - 2\} \qquad [35]$$

from which we see that the slope of the linear expression is very modest.

Thus, environmental variance does pose a more severe obstacle to population persistence than does individual variance, and this

obstacle is not readily circumvented by modest increases in the
population ceiling.

NUMERICAL RESULTS

a. Influence of maximum population size on mean persistence time

The discussion of the reparametrized version of the general
birth and death model resolved three factors which will determine
the expected time to extinction. These are the population ceiling,
the schedule of mean growth rates at each population size, and the
schedule of variance in the growth rate at each population size.
The two schedules may themselves be represented as parametrized
functions.

We might conveniently treat the mean growth rate on the one
extreme as a constant unaffected by density, or on the other as a
value which declines linearly with density, reaching zero at the
population ceiling (expressable, conventionally in terms of a zero
density rate $r(0)$ and the ceiling k). The schedule of variance is
conveniently decomposed into an individual component and an
environmental component, and these might, under various scenarios,
be represented as density dependent or density independent, as
will be discussed in a moment.

Here we begin an exploration of the response of persistence
time in the parameter space defined by the above factors. In
Figure 1 we show the response to mean growth rate (r) and
population ceiling (k), where the growth model is density
independent, the variance in growth rate conforms to a model where
all the variance is due to independent individual variation and
this variation is constant (density independent) corresponding to a

value of 1.0 for the parameter Vl. To recapitulate the interpretation of this variance: it represents the variance we would expect to observe between individuals if we made simultaneous measurements of the growth contributions of many individuals over a very short time interval in a constant and uniform environment. If, hypothetically, the distribution were normal, a variance of 1.0 would correspond to a distribution where 95% of the observed instantaneous rates would be less than r+2.0 and greater than r-2.0.

The contours representing persistence times in Figure 1 are labeled at intervals corresponding to powers of 10. That these contours are relatively evenly spaced in the horizontal indicates that the expected persistence time is related more or less to the power of population size--as predicted by approximate equation (5). We see that the dependence on r is slight for the very smallest population sizes, but that as the population ceiling becomes even of modest magnitude, there is an appreciable effect of r, especially in the range of small r.

Further we note that with this assumption of individual sources of variance only, the expected time to extinction becomes very large at quite modest population sizes provided the mean growth rate is reasonably large. However, at mean growth rates of just a few percent per year (as might be the case for many large mammals), an expected time to extinction of say 1000 years will require a fairly substantial maximum population size, that is more than 50, when the variance is of the magnitude in this example.

Figure 2 represents a similar contour plot of expected time

to extinction against a mean growth parameter and population ceiling, for individual variation only with variance equal 1.0, only here the model is density dependent, with linear (logistic) decline in the realized mean growth rate with population size, so that the growth parameter actually represents r(0) (whereas in Figure 1 it represented r). We find a similar power function form to the response surface, but the magnitudes of the persistence times are greatly reduced.

On reflection, it may not be reasonable to maintain a contstant variance attributable to individual variation whilst the mean growth rate is declining linearly to zero. For example, if the reduction in growth rate is brought about by a decline in birth rate, we might expect the variance between individuals to decline also (but not to zero). For example, if V1 declines linearly to half its zero density value at n=k, with the model otherwise identical to that of Figure 2, we obtain the plot of Figure 3. The expected persistence times, with density dependence, in Figure 3, are very close to those with density independence in Figure 1. We conclude that density dependence may not be terribly important to our calculation of time to extinction in small populations, provided the variance in the growth rate declines in a manner that is commensurate with the decline in mean growth rate, as density increases.

In Figure 4 we show the response of persistence time to mean growth rate (r) and population ceiling (k), where the growth model is density independent, as in Figure 1, but with all the variation in growth modeled as environmental variance, and this variance is

constant corresponding to a a value 1.0 for the the parameter V(env), as contrasted with Figure 1 where V1 was 1.0. To recapitulate the interpretation of this variance: it represents the variance we would expect to observe between sample determinations of the growth rate, taken at different times, where each sample spanned a very short time interval, but with each sample including sufficient individuals that the contribution of variation between individuals would be negligable.

Comparing the contour plot of Figure 4 with Figure 1, we find that with environmental variance the time to extinction is much shorter and it is much less responsive to the maximum population size. Whereas the contours in Figure 1 were labeled at intervals corresponding to powers of 10, in Figure 4 they are labeled at arithmetic intervals. We see, that with environmental variance, the expected extinction time, far from increasing exponentially with k, increases more or less linearly with k, as predicted by our approximate inequality (34). A trully massive population ceiling would be required to achieve a reasonably long time to extinction when the environmental variance were of the magnitude in this example.

More extensive numerical exploration of the determinants of persistence time, with this model, will be presented elsewhere.

We conclude from our initial exploration that the variance in the population growth rate, and especially that component of variance owing to environmental variation, will probably prove to be the critical element in determining the mean extinction time for a given small population whose mean growth rate is positive.

Further, to the extent that the variance is dominated by environmental variance, the response of persistence time to the size of the population ceiling will be very gradual, rather than exhibiting an appearance of a dramatic threshold.

b. The distribution of persistence times

The machinery described in the preceding sections conveniently calculates a mean time to extinction. This does not tell us how representative the mean might be. To explore this latter question, we undertake a much less convenient course of simulation (for which, incidentally, the birth and death process is rather awkward).

The central algorithm of the simulation begins by first sampling an exponential distribution, the parameter of which is $[b(n)+u(n)]n$ as calculated from specification of expected growth rate and variance in the growth rate, to obtain the time to the next demographic event. This is followed by sampling a binomial, the parameter of which is $b(n)/[b(n)+u(n)]$, to determine whether the event is a birth or a death. Accordingly the population increases or decreases, and the elapsed time is accumulated until the population reaches zero. Each simulation is initialized with a population at its ceiling.

Figure 5 shows a histogram of extinction times for 1000 such trials of a population model where: the population ceiling is 20; the mean growth rate is 0.05, with no density dependence; the environmental component of the variation in growth rate is 0.25, expressed as a standard deviation (i.e., the square root of V(env) of equation [21]); and the individual component of variation,

expressed as a standard deviation in a population of 1 in a constant environment (i.e, the square root of V1 of equation [21]), is 0.5. The mean persistence time in this simulated sample was 122.6, compared to the calculated theoretical expectation of 121.4 from equation (12).

The distribution is strongly skewed right. This, in concert with the observation that the standard deviation (103.4) is rather near to the value of the mean, suggests an exponential distribution. Transforming the values by raising e to the negative power of the observed value divided by the mean would, for a true exponential distribution, result in a uniform distribution in the range 0 to 1. The transformation performed on the sample from the simulation resulted in the histogram of Figure 6, which is rather like a uniform, indicating that the distribution is rather like an exponential in this example.

For an exponential distribution the median value is ln(2) times the mean. Thus, if it is true in general that the persistence times in the birth and death process are distributed more or less like an exponential random variable, we may expect the median persistence time to be about 70% the mean. This is another way of saying that a large fraction of the extinctions will take place after elapsed times that are considerably shorter than the mean.

MANAGEMENT IMPLICATIONS OF DEMOGRAPHIC EFFECTS

As in many practical matters, we would wish, in the minimum viable population problem, for some simple rule of thumb, stating that above a particular magic number the population is rather safe from chance extinction, whilst below the magic number the

population is very vulnerable. Our analysis indicates that, prima facie, no such number is forthcoming, for the expected survival time depends critically not just on the population ceiling but also on the mean population growth rate and on the variances in population growth rate. Further, for some portions of the parameter space, the relation between mean survival time and population ceiling is very gradual, so that what we mean by a large enough population will depend critically on what we mean by a long enough survival time.

Shaffer (1981) has tentatively suggested, for a starting definition, that the minimum viable population be that which has a 99% probability of surviving 1000 years. The form of this definition addresses the matter of linking the required population ceiling to a specified parameter of the distribution of survival time. We must note here, however, that the particular values suggested will, from a social standpoint, prove extremely stringent. We observed that a simulated distribution of extinction times, under a plausible birth-and-death-process model, had a standard deviation that was of a magnitude comparable to the mean, with a substantial skew right, so that a 1% tail corresponding to 1000 years will imply an enormous mean survival time, which may require correspondingly enormous populations if the growth rate mean and variances are at all unfavorable.

As regards computing the effects of mean growth rates and variances in growth rates, we find that once we do have estimates of their magnitudes, the mathematical machinery of the preceeding sections will make it quite simple to obtain an estimate of the

minimum population ceiling required to achieve a specified mean
time to extinction. The estimation of a mean growth rate is not an
uncommon component of ecological research and population
management, though this is not to say that the practise is free of
pitfalls (c.f. Goodman, 1984). The estimation of variances in
growth rate in a natural population, with partitioning of that
variance into individual and environmental components, probably
has never been undertaken in quite the form described here. In
principle, it can be done, as will be illustrated in analysis of a
simulation of an age structured population model with seasonal
reproduction, to be presented elsewhere. In the actual event, it
will prove a considerable task for each case, since the
observations must span a long enough period of time to sample
adequately the long term environmental variability.

Inevitably, there will also be some controversy about
assumptions which will have to be made about the relation between
the observed central mass of the distribution of environmental
variation and the tail of the distribution corresponding to events
too rare to appear in a feasible sampling program but which are
still common enough that they bear on the stipulated time horizon
for survival. This problem is by no means unique to our present
endeavor. Gumbel (1958) quotes a presidential commission to the
effect that: "However big floods get, there will always be a
bigger one coming; so says one theory of extremes, and experience
suggests it is true."

Though it may be difficult to obtain good estimates of the
environmental variance, it will often be relatively easy to

determine whether the population's circumstances correspond to a portion of the parameter space where the environmental variance is extremely important to the survival time. Where the effect of variance is small enough that there would be practical benefits from small increases in the mean growth rate, management measures could concentrate on that aspect of demography (Goodman, 1980).

Where the role of environmental variance is overriding, there will be merit to considering management measures that effectively reduce the variance--most especially when there is reason to suspect that in the absence of such intervention the required minimum population ceiling is too large to be a social reality. Such measures might include, suplemental rations, predator control, disease control, habitat modification, etc., implemented only at times when the population is declining too rapidly or is too small. Arriving at optimal schedules for implementing such interventions will be an interesting exercise in operations research.

This idea of systematic intervention in natural areas is somewhat at odds with the present philosophical stance of the Park Service, for example, but these attitudes might well change when the need is documented. A potential debate over whether extinction is natural may provide temporary diversion.

Programs of reintroduction may be viewed as special cases of variance management. Reintroductions are often portrayed as singular efforts, which need not be repeated. M~~y successful reintroductions, such as the redistribution of elk and pronghorn antelope earlier in this century, and of peregrine falcons very recently, seem more or less to be of this one-shot nature, but of

course we are saying this from a rather short time perspective. In a longer perspective we might think of these introductions as part of a program which augments the species population whenever its local density becomes too sparse, as indeed is commonly done when, for example a particular reintroduction "fails." The captive breeding program for California Condor, now underway, is likely to lead to an indefinite program of release of captive-bred birds to the wild, in an attempt to supplement deficient wild recruitment which very possibly will continue to be deficient indefinitely.

Taking the view that particular reserves for particular species, if left to themselves, may well have unnacceptably high extinction rates individually, we come to the strategy of augmenting dwindling populations, or replacing lost populations, locally, with individuals moved from other reserves where, at that moment the population is nearer its local ceiling. The essence of this strategy is variance minimization. Judging the ensemble of reserves, among which the reintroductions are taking place, we naturally come to the the classic question in reserve design, whether a single reserve of total carrying capacity equal to the sum of the multiple reserves would be better or worse judged in terms of the expected time to extinction.

From the standpoint of our discussion of chance demographic events, and assuming that the habitats in consideration are of equivalent quality, the answer to the question depends on whether the environmental variance operating on the separate reserves is to some extent independent, while the environmental variance in the single large reserve is identical to that of any one of the

smaller reserves. If the separate reserves exhibit at least partial
independence, then over the ensemble of reserves the environmental
variance will be less than that of the single large reserve, so
the design of several reserves, linked by a transportation
program, would be superior to a single large reserve.

In the absence of a transportation program, the comparison is
slightly more complicated. Owing to the smaller population size on
each of the multiple reserves, the mean time to extinction on each
would be less for these than for the single large reserve. But
since we hypothesized that they are independent, the time for all
of them to reach extinction is greater than the average time for
one to do so. The simple solution to this puzzle is to envision
each of the multiple reserves as one "individual" subject to a
birth and death process model in which all the variance in growth
rate was individual; and groups of the same size quantum in the
single large reserve are likewise treated as "individuals" in the
model. Here we immediately see that subdividing is
disadvantageous, for the dynamics in the ensemble of small
reserves will be those of a pure death process, whereas the single
large reserve will have the dynamics of a birth and death process
where the death rate is identical to, or smaller than, that in the
multiple reserve ensemble (depending on the degree to which the
aggregation into units is literal or figurative) and the birth
birth rate is non zero whenever the number of "individuals" is less
than the total number of smaller reserves.

It is hard to imagine the motivation for a deliberate policy
forbidding reintroductions in a system of multiple reserves, but

the above example does make clear that there would be a definite cost to neglecting the transportation program in a multiple reserve system, as that would result in an expected survival time which is less than could be expected on a single reserve of equal area, whereas with a proper transportation program the multiple reserve system would have a greater expected survival time than the single large reserve.

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EXTINCTION TIME (CONTOURS)

POPULATION CEILING (k)
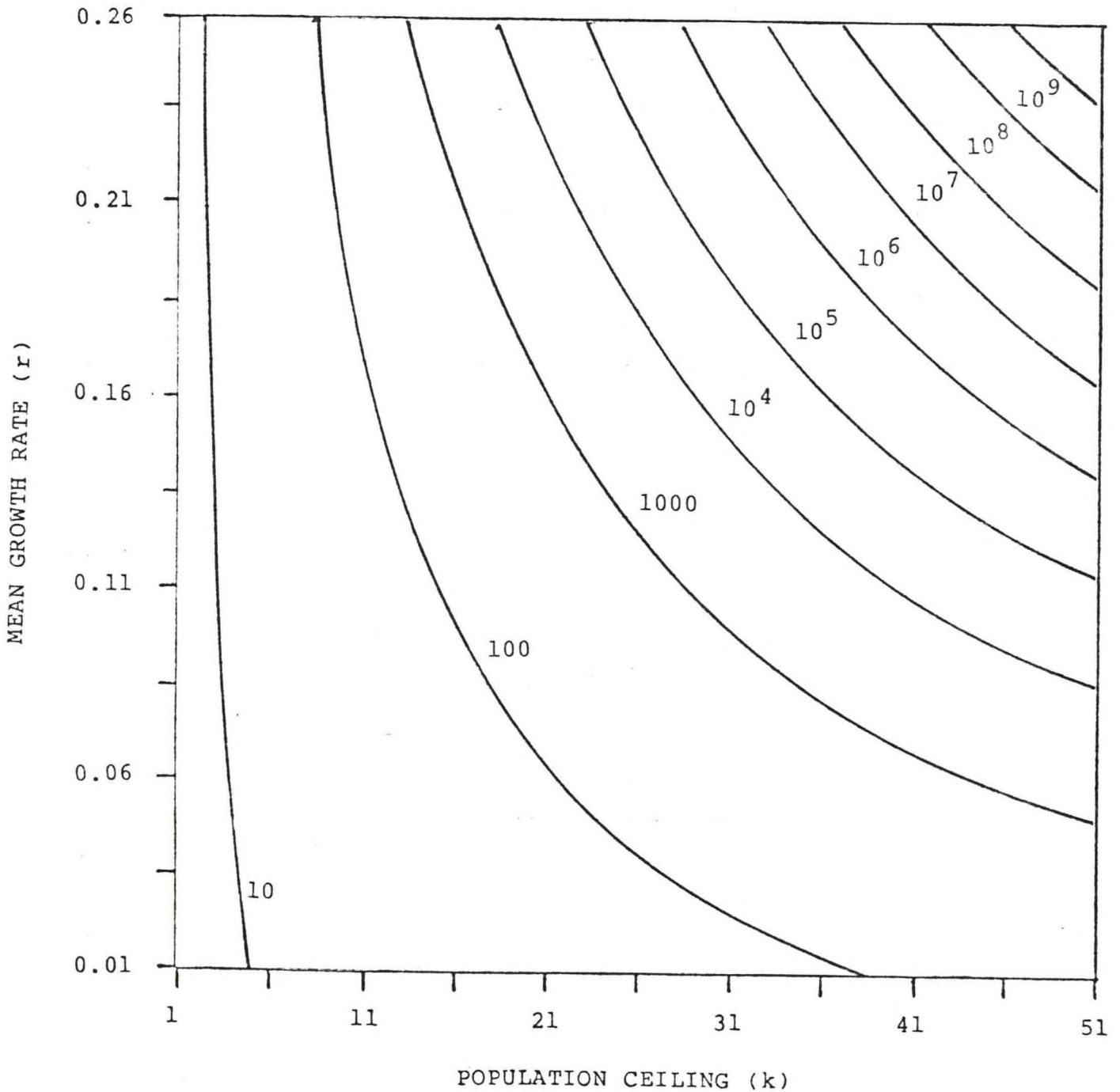
Figure 1. Plot of mean population persistence time (contours), as a
function of the population ceiling (k) and mean population
growth rate (r), in a model with no density dependence, no
environmental variance, and with the between-individual
variance in r being unity expressed on the basis of a single
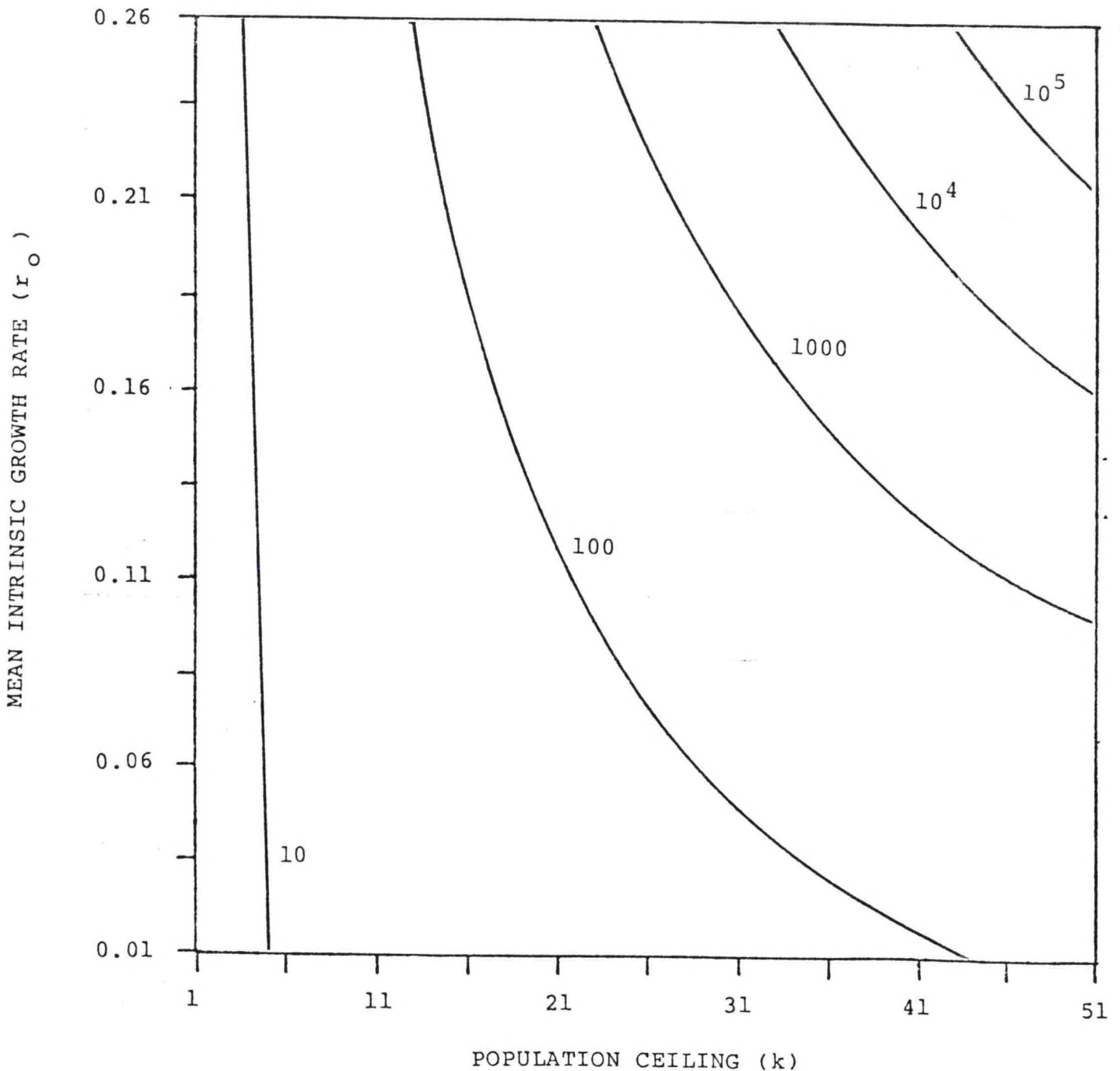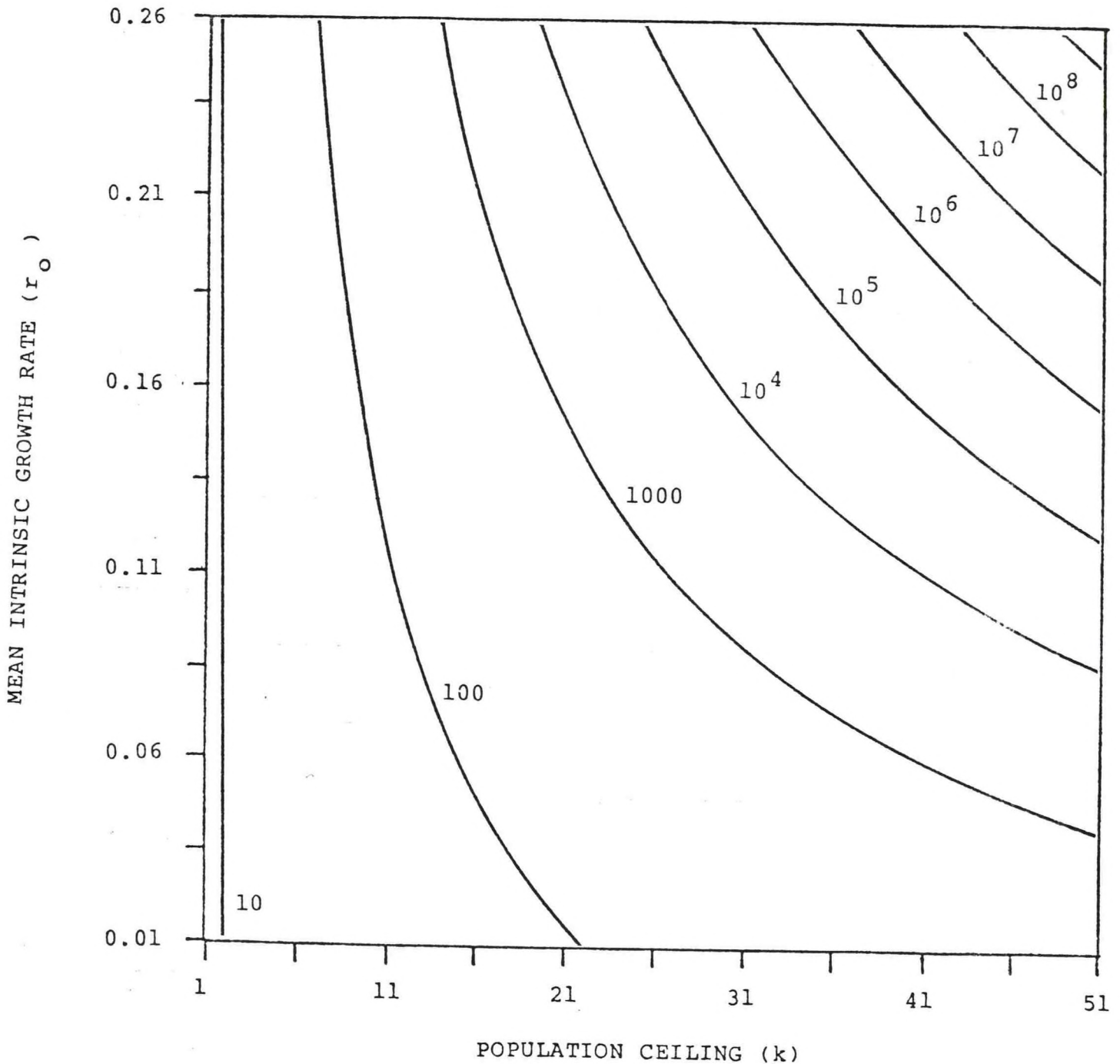individual (V1).

EXTINCTION TIME (CONTOURS)

Figure 2. Plot of mean population persistence time (contours), as a function of the population ceiling (k) and mean population growth rate of a vanishingly sparse population (r(o)), in a model with linear density dependence of the mean growth rate at each density, no environmental variance, and with the between-individual variance in r being unity expressed on the basis of a single individual (Vl).

EXTINCTION TIME (CONTOURS)

Figure 3. Plot of mean population persistence time (contours), as
a function of the population ceiling (k) and mean population
growth rate of a vanishingly sparse population (r(o)), in a
model with linear density dependence of the mean growth rate
at each density, no environmental variance, and with the
between-individual variance in r being unity in a vanishingly
sparse population (expressed on the basis of a single
individual) and declining linearly with density, to a value of
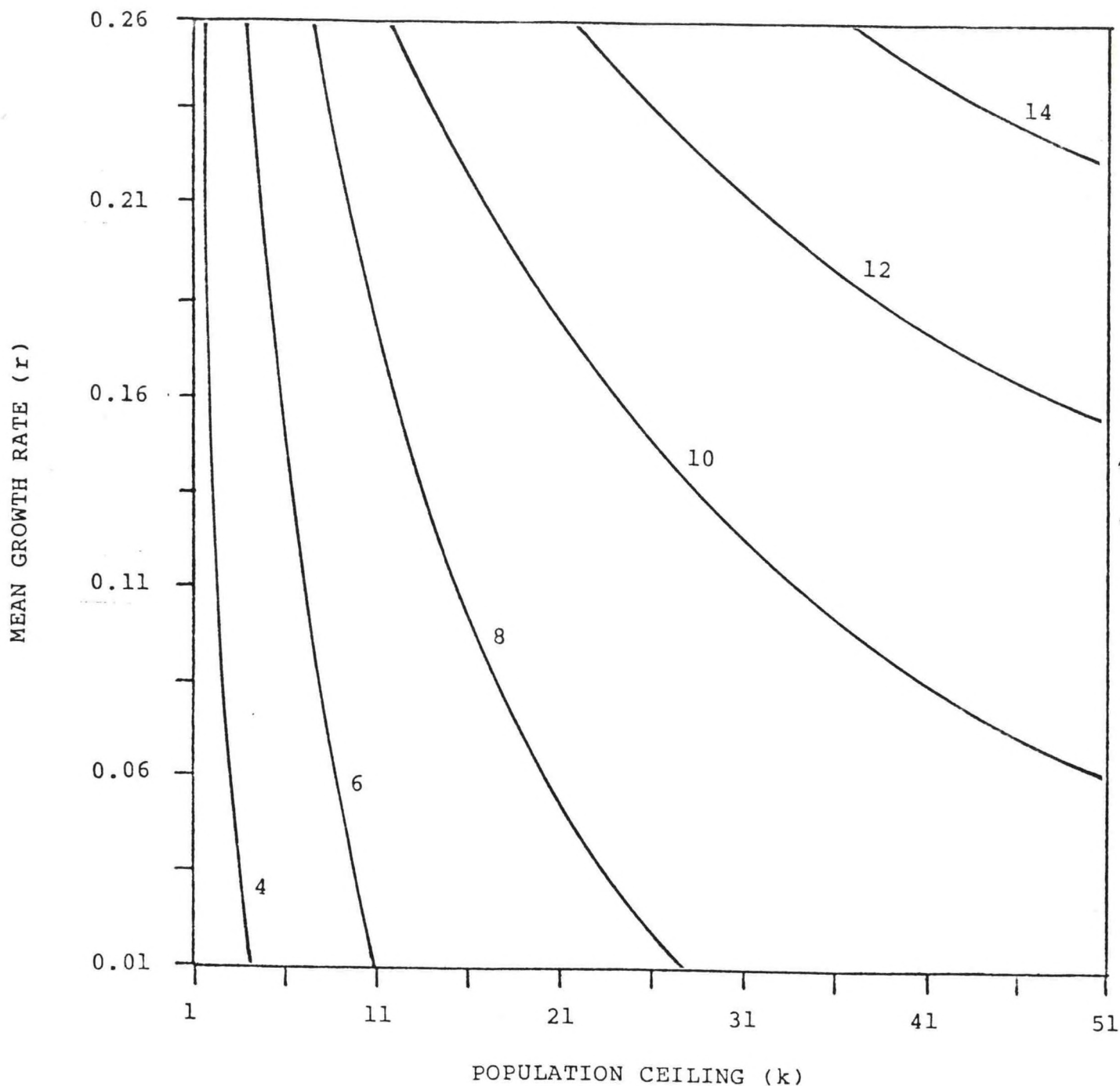one half at the population ceiling.

EXTINCTION TIME (CONTOURS)

Figure 4. Plot of mean population persistence time (contours), as a
function of the population ceiling (k) and mean population
growth rate (r), in a model with no density dependence, no
between-individual variance in r, and with the environmental
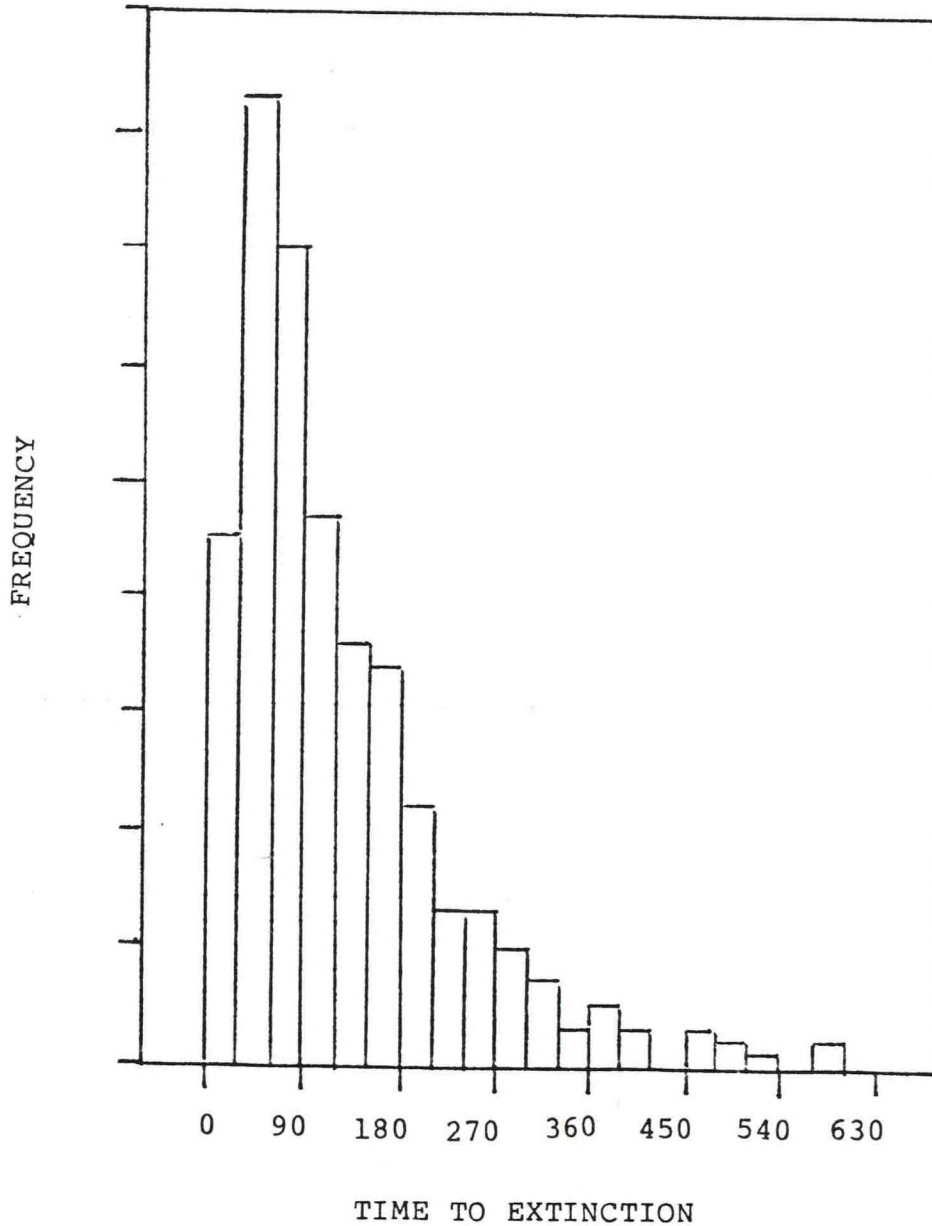variance in r being unity.

Figure 5. Histogram of time to extinction in 1000 trials of a simulated birth and death process, in a model with no density dependence, where the population ceiling (k) was 20, the mean growth rate (r) was 0.05, the variance component in r owing to the environmental variation corresponded to a standard deviation of 0.5, and the variance component in r owing to between-individual variation corresponded to a standard deviation of 0.5 expressed on the basis of a single individual ($\sqrt{V1}$).
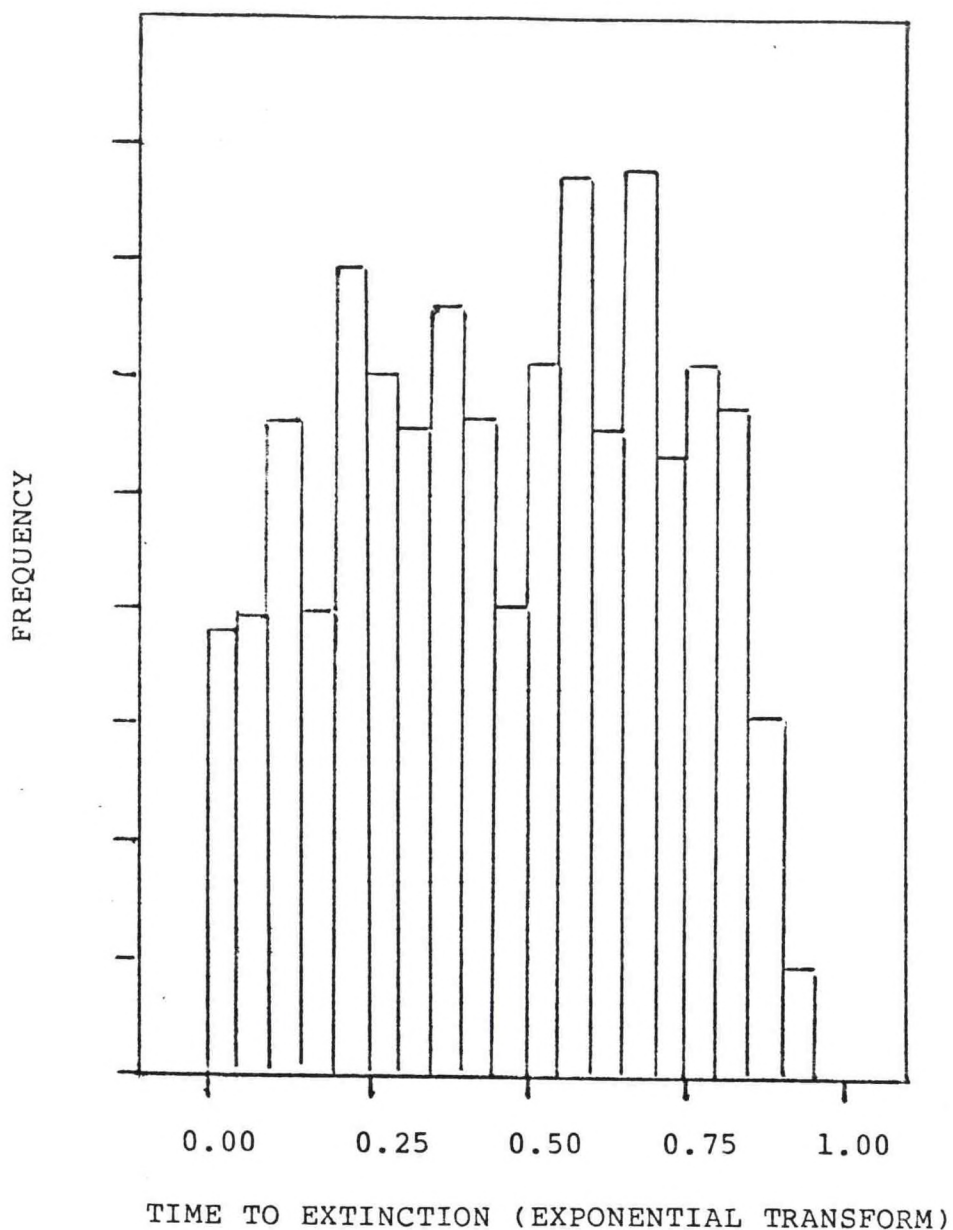
Figure 6. Histogram of the times to extinction from the simulation shown in Figure 5, where the times have been transformed in a manner that would transform an exponentially distributed variable to a uniformly distributed variable on the interval (0,1) as explained in the text.