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### **"Viability Analysis of Endangered Species: A Decision-Theoretic Perspective"**

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**These are preliminary lecture notes, intended only for distribution to participants.**

VIABILITY ANALYSIS OF ENDANGERED SPECIES:

A DECISION-THEORETIC PERSPECTIVE

by

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## **ABSTRACT**

The concept of population viability is probabilistic in nature, usually being expressed through such indicators as "expected extinction time", or "probability of survival for 1000 years". Such one-dimensional indicators might be adequate to characterize empirically-derived extinction risk in steady-state circumstances, such as in a long-established and undisturbed reserve. But they do not serve as well for evaluating viability in dynamically changing environments, nor for appraising the circumstantial evidence of risk provided by computer simulation of a stochastic population model.

To characterize risk adequately in these circumstances requires describing a qualitative pattern of risk, sorting out short-term effects, due to initial population size and environmental state, from longer-term effects related to the character and quality of habitat. Furthermore, the relevant time-scales for the analysis depend upon the processes of change present in the habitat, including persistent effects from deliberate or inadvertent anthropogenic habitat manipulation.

In the present study, alternative extinction risk indices and sustainability profiles are suggested, appropriate for formulating a risk management strategy in a dynamically changing environment. The concepts presented are applied to the problem of viability assessment of the endangered Northern Spotted Owl, in the harvested temperate rainforest landscape of the U.S. Pacific Northwest.

Key Phrases: Population viability analysis, managing endangered populations in changing environments, extinction indices vs. sustainability patterns .

Key Words: Endangered species, hazard profile, conditional survival profile, Bernoulli valuation, Northern Spotted Owl.

## 1. Introduction

Computer-simulation modeling of the dynamics of small populations has become a central, perhaps indispensable, tool for the management of endangered species. Because of the limitations of more direct, empirical studies--one seldom has duplicate populations in the field, with which to experiment or from which to collect survival statistics--viability assessments necessarily must fall back on evidence of a more indirect and circumstantial nature.

One of the most widely used approaches has been to experiment with artificial populations, existing only within a computer's dynamic memory. With these it is easy to undertake many "experimental" runs of a population's evolution over time, collecting survival statistics or investigating the effects of deliberate management interventions.

These computer simulation models typically incorporate a variety of relevant stochastic elements, such as random environmental fluctuations, random demographic variability, risk of catastrophic events, etc. It is in the nature of such models that they predict ultimate extinction for any population under continuing risk. (See Appendix A1.) Consequently one cannot speak of attaining absolute security against extinction, but must describe viability in more limited terms, incorporating some probabilistic measure of "population persistence" [Ludwig, 1975].

Typically these measures have been scalar quantities related to the random time-of-extinction  $T$  of the population. Classically, [e.g. Richter-Dyn and Goel, 1972], the scalar indicator of  $T$  had been its expectation  $E[T]$ . More recently favored has been the probability of survival to a specified time horizon  $T_0$ , i.e.

$$\text{prob}[T > T_0],$$

[Shaffer, 1983, Salwasser et.al. 1983].

Such indices are useful as measures of comparative risk, but the numerical values arrived at through computer simulation ought not to be construed as providing quantitative predictions, to be applied literally in real-world conservation decisions. While a computed index value is (within sampling error) an accurate, if incomplete, statistical characterization of the artificial computer population, its numerical significance for the real-world population is unknown, and in principle is unknowable.

On the other hand, the output from a computer simulation model can exhibit a rich qualitative structure which, if the mechanisms in the model are empirically-based, is likely to prove robust through many model refinements and elaborations. Furthermore,

that structure, much of it probabilistic in character, can provide substantial insight into the likely qualitative effects that alternative management strategies would have on the real-world population's viability.

The present article pursues this perspective through several phases. Throughout, we emphasize the decision-theoretic context of the analysis, in which achieving a level of protection, against population degradation or even extinction, is to be balanced against other conflicting societal goals. We begin by suggesting a way of replacing a single scalar index of viability by a more complete temporal pattern of hazard, a system description with qualitative as well as numerical content.

Next we examine viability patterns that involve population characteristics other than extinction time  $T$ . These may provide considerable additional insight into the likely implications of a choice made among decision alternatives.

Finally we reconsider the ramifications of a single decision as a stage in a temporal decision process, insisting that each decision stage should be evaluated in reference to the degree of its reversability and the persistence of its effects. This leads us to reexamine scalar indices (Bernoulli indices), and to emphasize a class of these that may be particularly relevant for evaluating actions with attenuated effects. Once again, the single index may usefully be extended to a full temporal pattern.

These general concepts are illustrated through application to a specific Markov chain model, describing the population dynamics of the endangered Northern Spotted Owl. Then, in a series of appendices, the theoretical principles which underlie the analysis are made precise and analysed mathematically. These appendices also include the necessary formulas for practical calculation of the various viability criteria developed in the article.

We note that all of this discussion still abstracts from a population's spatial heterogeneity, as does the illustrative Owl model. This spatial aspect of viability decision analysis will be the subject of a second article, which is now being planned.

## 2. The Owl Model

To make our discussion concrete, we shall illustrate the general concepts through application to a specific model, one developed to examine the population viability of the Northern Spotted Owl in the mature ("old growth") temperate rain forests of the Pacific Northwest. [Lamberson, McKelvey, Noon and Voss, 1992].

The model is based on the known life-history characteristics of the Owl as a long-lived territorial species, whose population dynamics are driven by stochastically-variable annual fecundity, (the result of fluctuating food supply), and variable dispersal success, (depending on the availability and accessibility of suitable old growth home territories). The latter depends in turn on the degree of fragmentation of the bird's forest habitat. In a badly fragmented habitat, dispersal success will be low, and the population dynamics can be expected to show a critical threshold of population size, below which continued survival is at high risk (Allee effect--see section 4.).

The model describes Owl demography through a simple set of stochastic difference equations, tracking the population by means of an annual census of territorially-established solitary males and of nesting pairs. The spatial heterogeneity of habitat is suppressed in this simple model, with habitat quality being expressed by a single parameter, namely, the percentage of old growth forest it contains. The model incorporates a stylized dispersal process, describing search by juvenile males for suitable unoccupied territories, and search by juvenile females for established males.

Model parameters include juvenile and adult survival rates, stochastic fecundity, search efficiency, and habitat quality (characterized as % old growth). These are chosen to fall within the range of the biologist's current best estimates, and their sensitivity has been explored.

The model has been studied extensively, by mathematical analysis of its structure and statistical analysis of repeated simulation runs. Details of that work are described in the article cited above. We include here a TurboPascal computer program of the basic demographic model, along with a list of parameter values used in the various figures shown.

### 3. Trade-Offs Among Incommensurates

In the Spotted Owl illustration, the central management issue is how to protect the Owl while maintaining the traditional logging industry in the Northwest's temperate rain forest. The trade-off can be presented succinctly in a single graph (fig.1). This graph plots the probability of 250 year owl population survival as a function of the percent of old growth maintained in the forest. (Recall that, in this model, old growth is always distributed uniformly throughout the forest.)

Each axis of the graph represents a quality valued by society. The vertical axis (250-year survival probability) is a measure of the viability of the population at risk. It may also be regarded

as an indicator of the health of the forest ecosystem.

The horizontal axis (percent old growth left standing) also measures the amount of forest that is to be dedicated to sustained harvest. As such it represents a direct market value, but also may be regarded as a crucial element in sustaining the traditional harvest-dependent way-of-life of small forest communities.

Thus it seems unlikely that the values in either axis can be fully captured in market-based monetary terms. Their trade-off will be a societal policy decision, achieved through the political process. Furthermore, as represented in the graph, the trade-off is zero-sum: one cannot improve the status of either value without diminishing the other.

A number of environmental and resource economists [Ciriancy-Wantrup 1968, Shackle 1969, Bishop 1978] have argued for protecting non-monetary ecological, environmental, and aesthetic values, by maintaining specified "minimum security levels" for them. Thereby these values would be given priority over more conventional market values, which are to be optimized through benefit-cost trade-offs, but only within the specified security constraints.

In protecting against risk of population extinction, such a preemptive minimal standard would necessarily be probabilistic in nature. Thus for example a minimal standard involving expectation of extinction might specify that  $E[T]$  exceed one thousand years.

Alternatively, Shaffer [1983] advocated setting a minimal standard on survival probability to a specified time horizon, of the form we have adopted here, e.g. that

$$\text{prob}[T > 250] > .95.$$

Shaffer pointed out that, in specifying such a standard, both the time horizon (here, 250 years) and the security level (here, 95%) are arbitrary, and that neither can be arrived at on purely scientific grounds. Both choices, he asserts, "while amenable to scientific advice and guidance, require a value judgment by society".

One can interpret current U.S. law (the Endangered Species Act), as establishing Owl survival to be a preemptive value, calling for a minimal security level in the sense described above. In principle, one should set the security level for population viability without any consideration of economic costs, such as the impact on timber harvest. Only within the constraint so imposed should one then undertake measures for protecting

competing values, such as the timber industry's stability and economic efficiency.

In practice, of course, society will look at the two axes together and choose a compromise, one that is not likely to be entirely satisfactory to either party to the dispute.

The scientific task here is to describe, clearly and fully, the ramifications with respect to all societal goals of the available choices. On the other hand, it must be recognized that, by choosing a particular index of Owl viability as we have done, we have already framed the terms of the debate. The scientific issue then is whether we might have done this in a better, more informative way, by presenting qualitatively a more complete description of extinction risk than a single suspect number can provide.

#### 4. The Bayesian Perspective: The Value of Information.

Before examining further the decision-theoretic context for selecting viability measures, it is desirable to examine briefly certain underlying principles of inference. To be concrete, we turn again to the Owl model.

One feature of this model is its sensitivity to the dispersal process, and to the impact of low habitat density on dispersal success. This feature manifests itself through the presence, in the simulation output, of a sharp threshold in the graph of survival as a function of old growth density. For old growth levels below the threshold (which occurs around 20% in figure 1), 250-year survival is quite low; above it survival probability rises quickly to nearly one. Because of its explicit biological basis, this "Allee effect" is likely to be robust across a range of models.

On the other hand, the precise location of the threshold, in terms of old growth level, is very model-specific. In fact, even in the present model, the location of the threshold is affected substantially by changes in the model's parameters, specifically those which specify the Owl's dispersal search efficiency and the stability of its food supply. Figure 2 illustrates the changes in threshold locus that can result by varying these parameters, within the range of our current uncertainty over their true values.

How ought one to deal with such differing predictions? In effect, two forms of uncertainty are manifest here: uncertainty within and uncertainty across models. The within-model uncertainty is due to process stochasticity, and is captured through frequency counts in simulation replications. The



between-model uncertainty is due to measurement error in the parameters, which are presumed to possess "true" numerical values which we do not precisely know.

Despite these differences, classical decision-theory adopts a "Bayesian" perspective on uncertainty, whereby the probability of an event is taken as measuring only one's strength-of-belief in its occurrence [DeGroot, 1970, Maler 1989]. One thus treats the two sources of uncertainty on a par. In effect, Bayesian Decision Theory is willing to contemplate a "lottery" of models, with expectations for the lottery formed according to the usual rules of probabilistic averaging.

Hence, if the two extreme curves in fig.2 are regarded as being representative and equally likely, they may be combined by simple averaging. Thereby one arrives at an overall 250-year expected survival curve--one with a much less abrupt threshold than that present in either of its component curves.

An alternative perspective, one likely to be favored by environmentalists, is to protect against the "worst-case possibility", in this instance against the curve to the right in fig.2. Adherence to this "precautionary principle" [Shackle 1969, Perring, 1991] has further justification in the irreversibility of population extinction, should that event occur.

In either perspective, there is an advantage to be gained for society by narrowing the uncertainty in the model's parameter values, both to decrease the risk to the Owl and to increase flexibility in managing the timber harvest. Such improved knowledge can be gained, at a cost in time and money, and the decision to pursue it is an available choice in the management process. [Raiffa 1968].

##### 5. The Dynamic Decision-Process: Sustainability.

Shaffer emphasized the need to decide upon the appropriate time horizon for survival, but he did not suggest how this might be done. Certainly the choice of horizon can significantly affect the character of the results displayed. In figure 3, for example, one sees how, in the case of the Owl model, changing the time horizon affects the shape of the survival curve as a function of % Old Growth. Note in particular that, as the horizon is lengthened, the location of the threshold shifts and the threshold itself is softened.

Of course what we are observing as we lengthen the horizon is, for each fixed level of Old Growth, a sequence of points, increasingly remote in time from the present, on the survival probability time-profile--the complement to the probability

distribution for the random variable  $T$ . Figure 4 shows this survival time-profile for 25.5% Old Growth and a variety of initial Owl population levels. A characteristic property of all such profiles is that their shape, for asymptotic time, approaches a geometrical decline [Appendix A2].

In a decision-theory context, the determination to specify Owl survival at the 250 year horizon might reflect a view that a harvesting error made today could be corrected within a 250 year time span (for example, by allowing young forests to mature). This may be so, provided the species does not become extinct in the interim! Thus, accepting a choice of current Old Growth level entails accepting a certain level of risk to Owl viability during the next 250 years.

This perspective leads to a perception of population viability as a dynamic quantity, tied to the status of the population at a current point in time and to the management actions initiated at that time. Monitoring of sustainability of the population therefore requires periodic updating of the viability index, to take account of the evolving status of the population, and to project population vulnerability over the subsequent time era.

These considerations lead us to advocate introducing, into population viability analysis, the concept of hazard over time. Specifically, the  $\tau$ -Year Hazard Profile  $H_\tau(t)$  is the probability that, for a population that has survived to time  $t$ , the population will become extinct within the next  $\tau$  years:

$$H_\tau(t) = \text{prob}(T \leq t + \tau \mid T > t).$$

Figure 5 shows the 250-year hazard time-profiles corresponding to the Owl survival time-profiles in figure 4. This figure shows clearly that the hazard level is influenced for a time by the initial population size. But that effect is transient, and after a certain lapse in time (in this case, about 450 years), the effects of initial conditions have washed out. Only the character of the habitat (e.g. the % Old Growth) then matters asymptotically. Of course, by the time transients have died out, the population may well have gone extinct! (From figure 4, survival to 450 years ranges from .1 to .5, depending on initial population.)

It may of course be objected that 250 years is too long a time horizon in this decision-theoretic context, in that potential trouble can be detected and corrected more quickly than that. Figure 6 shows the corresponding 100-year hazard profiles, which are seen to exhibit a similar behavior, and show that, at the time of the 250-year extinction peak, a disproportionate fraction of extinctions occur within the first 100 years.

We note that the asymptotic hazard level depends on aspects of habitat quality other than % Old Growth. Figure 7 shows how, for a fixed % Old Growth, asymptotic hazard depends on the level of stochastic variability in the Owl's food supply.

The behavior of the hazard time-profile, including its asymptotic constancy, is entirely general: It is characteristic not just of this specific Owl model but of all finite Markov Chain population models. [See Appendix A3]. It provides a tool for sorting out short-term transient risks, due to initial population status, from persistent risks related to habitat design. It suggests too the desirability of replacing the requirement of a minimal security level at a single fixed time horizon by a requirement of an upper bound on the height of the hazard profile.

## 6. Occupancy Values

Until now we have abstracted from the details of the population state at time  $t$ , retaining only the limited information contained in the survival profile, which specifies only extinction or non-extinction at each point in time.

But in fact a simulation run of the Owl model, or any Markov chain population model, provides much more information than that. It provides a complete description of a "sample path"  $\mathbf{x}$ , i.e. it specifies the complete state  $\mathbf{X}(t)$  of the population at each time step  $t$ , up to the time of extinction:

$$\mathbf{x} = \{\mathbf{X}(0), \mathbf{X}(1), \dots, \mathbf{X}(T)\}.$$

In the case of the Owl model, the "state" description at a particular time  $t$ , namely

$$\mathbf{X}(t) = [X_1(t), X_2(t)],$$

is itself a vector, specifying the number  $X_2(t)$  of nesting pairs and the number  $X_1(t)$  of solitary males established at territorial sites. A simple scalar measure of population size is

$$Y(t) = X_1(t) + X_2(t),$$

the site occupancy at  $t$ . A related viability measure is

$$\text{prob}[Y(T_0) \geq Y_{\min}],$$

where  $T_0$  is a chosen horizon and  $Y_{\min}$  is a chosen threshold.

In figure 8 we illustrate the use of this measure, specifically plotting

$$\text{prob}[Y(100) \geq Y(0)],$$

for a range of old growth and stochastic fecundity levels. Choosing the threshold at  $T_0=100$  to be equal to the initial population size is especially practical for large scale simulation models. This is because, without running the simulations beyond the first 100 years, one automatically is provided with a lower bound estimate of viability in the second (and subsequent) centuries as well:

$$\begin{aligned} &\text{prob}[Y(200) \geq Y(0)] \geq \\ &\text{prob}[Y(200) \geq Y(0) \mid Y(100) \geq Y(0)] \cdot \text{prob}[Y(100) \geq Y(0)] \geq \\ &\text{prob}[Y(100) \geq Y(0)]^2. \end{aligned}$$

It is instructive to compare the curves in figure 8 with those in figure 9, where we have plotted the probability of surviving (at any population level) to  $T_0=100$ . The substantially higher probabilities in figure 9 reflect the likelihood that many surviving populations at  $T_0=100$  fall below the threshold size. Significantly, the topological structures of the two figures are substantially different, implying different prioritizations by the two criteria.

If the same comparisons are made, but with horizon  $T_0=250$ , one finds a different result. Then the survival and threshold-attainment probability curves have the same topological structure, and it coincides with that seen in figure 8. This reflects the fact that by  $t=250$  the population distribution curves have approached their asymptotic shape (see below), and that the threshold-attainment probability structure at  $t=100$  already has anticipated the asymptotic topology.

Figure 10 shows the conditional-occupancy time profile for the owl model:

$$C\text{-Occup}(t) = E[Y(T) \mid T > t].$$

Note that, like hazard, this function is asymptotically constant. (Appendix 4). Indeed, the conditional probability density function of  $Y(t)$  assumes an asymptotically constant shape, which is illustrated in figure 11. The peak to the left of this curve shows the substantial risk of early extinction due to small current population size.

## 7. Ordinal Preference: Priorities over Distributions

In figure 12 are shown the survival probability distributions resulting when the Owl model is run under four different management prescriptions, involving two different (high and low) old growth densities, and two different fecundities (high and low, where high mean fecundity is accompanied by high fecundity variance). The results obtained reflect also the initial population size, which is taken to be the same in all four cases.

Assuming that all four regimes are attainable by habitat manipulation, one may ask: which should be regarded as preferable for advancing the goal of Owl viability?

Figure 13 shows the 100-year hazard curves for the same four management options. Taken together, the two sets of curves demonstrate the point that viability security is very imperfectly described by examining a single point on a survival profile, such as "survival until 250 years". From the figures, in the years at and beyond 250, the HI/LO option is clearly superior to the LO/LO option, both in raising current survival and lowering future hazard. But these positions are reversed during some of the earlier years, when current management actions will be having their greatest impact.

Similarly, the HI/HI option is superior to the LO/LO except in the first few decades. On the other hand, the HI/LO is superior to the LO/HI, according to both measures, at all points of time.

These insights are achieved by examining survival and hazard profiles together. However it should be noted that all the information being utilized is present already in the survival profile alone, since the hazard profile is calculated from it. [Appendix A3].

What is needed here is a means to integrate the information within each of the alternative survival profiles, to arrive at an overall preference ordering among them.

Such a preference ordering should conform to the usual rules of rationality. Thus if  $S_1$ ,  $S_2$ , etc. symbolize various attainable survival distributions, and preference for  $S_2$  over  $S_1$  is denoted by  $S_1 < S_2$ , then one would like at minimum that:

A) (Comparability) Any two distributions are comparable: either one prefers  $S_2$  to  $S_1$ , is indifferent between  $S_2$  and  $S_1$ , or prefers  $S_1$  to  $S_2$ . In symbols,

either  $S_1 < S_2$ , or  $S_1 = S_2$ , or  $S_1 > S_2$ ,

and

B) (Transitive Law)

If  $S_1 < S_2$  and  $S_2 < S_3$  then  $S_1 < S_3$ .

## 8. Bernoulli Preference Orderings

Both of the standard scalar measures considered up to now, namely I) survival to a time horizon, and II) expected extinction time, directly induce preference orderings that do conform to these rules: Namely, one should set  $S_1 < S_2$  when, respectively,

$$\text{I) } \text{prob}(T > 250 \mid S_1) < \text{prob}(T > 250 \mid S_2);$$

$$\text{or II) } E(T \mid S_1) < E(T \mid S_2).$$

Then conditions A and B may be verified immediately.

More generally, let  $U(T)$  be any cardinal utility function on outcomes  $T$ . Thus  $U$  is any non-decreasing function of extinction time. The expectation of  $U$  with respect to the survival profile  $S$  is

$U$  induces a preference ordering on survival profiles if one sets  $S_1 < S_2$  whenever  $E[U(T) \mid S_1] < E[U(T) \mid S_2]$ . We shall refer to preference orderings generated in this way as Bernoulli preference orderings.

$$E[U(T)] = \sum_{t=0}^{\infty} U(t) \cdot \text{prob}(T=t).$$

Note that both of the standard preferences orderings cited above are Bernoulli orderings: They correspond, respectively, to the utility functions

$$\begin{aligned} \text{I) } U_I(T) &= 0 \text{ for } T < 250, \quad U_I(T) = 1 \text{ for } T \geq 250; \\ \text{or II) } U_{II}(T) &= T \text{ for all } T. \end{aligned}$$

Certain attributes of these particular orderings may be considered to be objectionable:

I)  $U_I(T)$  is discontinuous: Survival through 249 years is assigned zero value; survival through 250 years is assigned full value--worth as much as survival through, say, 100,000 years.

II)  $U_{II}(T)$  is unbounded: Hence valuation is dominated by what happens at asymptotically remote times.

Of course, as we have noted, in a *decision-theoretic context* one or the other of these utility measures may be to some degree appropriate. However quite possibly one may do better with some other choice of utility measure. This is the issue we shall be exploring throughout the rest of this article.

Bernoulli preference orderings satisfy both properties (A) and (B) above, and also two additional properties of importance:

C) (Independence) A preference, say for  $S_2$  over  $S_1$ , holds independent of any probabilistic conditioning. More precisely, suppose that  $S_1 \preceq S_2$ , and that  $\alpha \cdot S_1 + \beta \cdot S$  represents a lottery of the distributions  $S_1$  and  $S$ , with respective probabilities  $\alpha$  and  $\beta$ . Then, for any  $S$  and any  $\alpha + \beta = 1$ ,

$$\alpha \cdot S_1 + \beta \cdot S \preceq \alpha \cdot S_2 + \beta \cdot S.$$

D) (Archimedean Property) If  $S_1 \preceq S \preceq S_2$ , then one will be indifferent between  $S$  and a certain lottery of  $S_1$  and  $S_2$ . That is, there exist probabilities  $\alpha$  and  $\beta$ , with  $\alpha + \beta = 1$ , such that

$$S = \alpha \cdot S_1 + \beta \cdot S_2.$$

According to the von Neumann-Morgenstern theorem [Owen, 1982], these four properties characterize Bernoulli preference orderings. That is, any preference ordering over survival probabilities which satisfies the properties (A-D), is Bernoulli. In particular, the Archimedean property reflects the scalar nature of the Bernoulli orderings--i.e. allowing reduction of the comparison of two time profiles to comparison of two real numbers.

In the following section we shall be examining Bernoulli utilities, other than the usual  $U_I$  and  $U_{II}$ , for appropriateness as indices of security and sustainability.

## 9. Cumulative-Value Utility Functions: Attenuation

Because of its scalar character, a Bernoulli ordering always does suppress much of the information contained in survival profiles. In this sense its appropriateness, for setting priorities, is inferior to comparing entire hazard profiles. However a Bernoulli ordering can, with the use of a single numerical index, capture some of the information most directly relevant to a particular decision. Where appropriate, this information can involve the entire time profile.

We shall call a utility function a cumulative-value utility when it is of the form

$$U(T) = \sum_{t=0}^{T-1} \pi(t),$$

where  $\pi(t) \geq 0$  for all  $t \geq 0$ . The latter condition is equivalent to requiring that  $U(T)$  be a monotone-nondecreasing function of extinction time. It is an entirely natural condition in

conservation biology, where the more delayed the extinction event, the better off we consider ourselves to be.

Writing  $U$  as a sum permits the interpretation of the individual term  $\pi(t)$  as the momentary value of population survival during the single time-step  $t$ .

In particular, if  $\pi(t) = a^t$ , for  $a < 1$ , we shall call  $U(t)$  an attenuated-value utility, with attenuation rate  $a$ . Such a utility seems appropriate in a decision-theoretic context, where  $E[U(T)]$  measures future viability resulting from current actions, and the influence of these actions gradually weakens over time.

Summing the geometrical series for an attenuated utility,

$$U_a(T) = (1-a^T)/(1-a).$$

It is easily verified that this utility incorporates an aversion to the uncertainties of future time, and indeed displays constant "relative risk aversion"  $\rho = -\Delta'U/\Delta U = 1-a$ . [Hey, 1979.] Note too that attenuation is formally equivalent to the economist's "discounting over time", though its rationale is different.

It is sometimes convenient to normalize this utility function to

$$V_a(T) = (1-a)U_a(T) = 1-a^T.$$

The normalized utility function  $V_a$  has the useful property that, for  $0 < a < 1$ ,

$$0 < V_a(T) \uparrow 1 \text{ as } T \uparrow \infty.$$

Hence  $E[V_a(T)]$  is less than or equal to 1, and increases with the persistence of the process.

The preference orderings, induced by Bernoulli attenuated utilities  $E[U_a(T)]$ , form a continuum for  $0 \leq a \leq 1$ . At the extremes are, when  $a=1$ , expected extinction time  $E[T]$ , and, when  $a=0$ , probability of survival to a finite horizon,  $\text{prob}[T > T_0 = 0]$ . Thus  $U_a(T)$  ranges from being non-risk-averse (with no attenuation), when  $a=1$ , to being wholly risk-averse (with instantaneously complete attenuation), when  $a=0$ .

Any one of these Bernoulli expectations provides a security criterion for evaluating a current action:

$$E[U_a(T)] = E\left[\sum_{t=0}^{T-1} a^t\right] \geq U_{\min},$$



or a sustainability criterion over a range of  $t$ :

$$CV_a(t) = E\left[\sum_{s=t}^{T-1} a^s \mid T > t\right] \geq CV_{\min},$$

$E[U_a(T)]$  may be calculated numerically in terms of the transition matrix of the underlying Markov chain. Furthermore, one may derive a procedure, useful in simulation, for iteratively calculating the conditional expectation  $CV_a(t)$ . (Appendix 5.) Figures 14-16 illustrate the application of attenuated utility to evaluation of the four management alternatives of section 7.

Figure 14 shows the (normalized) Bernoulli valuations  $E[V_a(T)]$  of the four options for a range of attenuation rates. Instead of measuring attenuation by the "attenuation rate"  $a$ , we have preferred the equivalent index  $V_a(250) = 1 - a^{250}$ , which measures the deterministic value accumulated in the first 250 years. Thus,  $V_a(250)$  increases with attenuation, approaching 1 as attenuation intensifies (i.e. as  $a \downarrow 0$ ).

For our application, it turns out that the preference ordering among the four options is independent of attenuation, below  $V_a(250) = .85$ . However, with greater attenuation than that, the survival rates in the very early years begin to dominate the index, and the preferences change.

This is confirmed in figures 15 and 16. We observe that, when  $V_a(250) = 0.9$ , the conditional valuation curves  $CV_a(t)$  do cross at early times  $t$ . Below about  $V_a(250) = 0.8$  the curves separate completely, and as attenuation decreases, the gaps widen.

## 10. Generalized Bernoulli Valuations

It is possible in many ways to assign a utility  $U(\mathbf{x})$  to a sample path  $\mathbf{x}$ --such an association is called a path functional. In this way one achieves a preference ordering among paths. Averaging probabilistically over the sample paths of the Markov Chain  $C$  yields a generalized Bernoulli valuation for  $C$  itself:

$$U^*(C) = E[U(\mathbf{x}) \mid \mathbf{x} \in C]$$

In a particularly simple case, the utility measure  $U(\mathbf{x})$  may be a function  $G$  of the state  $X$  at a single time horizon  $\tau$ :

$$U(X) = G[X(\tau)].$$

In section 6, we have already encountered several of these for the Owl model:

- 1) Site Occupancy:  $G_{occ}(X) = X_1 + X_2 = Y;$
- 2) Sited Population:  $G_{pop}(X) = X_1 + 2X_2;$
- 3) Survival:  $G_{surv}(Y; 0) = 0$  when  $Y = 0$  and  
 $= 1$  when  $Y > 0;$
- 4) Threshold Attainment:  $G_{thres}(Y; Y_{min}) = 0$  when  $Y \leq Y_{min}$  and  
 $= 1$  otherwise.

Note that

$$E[G_{surv}(X(\tau))] = \text{Prob}[T > \tau],$$

returns us to our earlier setting of valuing survival to a horizon. Up-dating of this criterion yields the hazard function:

$$E[G_{surv}(X(t+\tau) | T > t] = H_t(t).$$

Likewise,

$$E[G_{thres}(X(\tau))] = \text{prob}[Y(\tau) > Y_{min}]$$

returns us to our threshold criterion of section 6. Finally, the sustainability criterion, of conditional occupancy,

$$C\text{-Occup}(t) = E[G_{occup}(X(t) | T > t],$$

also was encountered in section 6.

The idea of cumulative-value utility measures also carries over to path functionals. A particular case is an attenuated value utility measure, of the form

$$U(X) = \sum_{t=0}^{T-1} a^t G[X(t)] + g[X(T)].$$

The corresponding generalized Bernoulli valuation is studied in Appendix A6, and is shown there, like the ordinary attenuated Bernoulli valuation, to have a closed-form representation in terms of the transition probability matrix of the Markov process.

In many other ways Generalized Bernoulli preferences behave like

the ordinary ones, for example in obeying the Von Neumann-Morgenstern rationality rules. One difference here regards lotteries: a lottery of Markov chains is not Markovian. Thus one must explicitly deal with the class of Lotteries of Markov Chains, rather than with Markov chains alone.

## 11. Conclusion.

It should be apparent that no single valuation measure is universally best: much depends on the application at hand. One generalization is that some measures contain more information than others, but even a complete time-profile, such as the hazard profile, is an incomplete description of the complete stochastic process. On the other hand, sometimes much relevant information can be captured in a single scalar index. The trick is to judge the information needs for the specific application, and choose accordingly.

## MATHEMATICAL APPENDICES

### A1. Discrete-Time Markov Chains

We shall restrict consideration to population processes which are represented as discrete-time Markov Chains, with a single absorbing state  $m=0$  (extinction) and transient states  $m \in S = \{1, 2, \dots, M\}$ . Similar results to those obtained in these appendices can be found also for continuous time Markov chains, including birth-and-death processes, and for diffusion processes. A general reference on applied Markov chains is [Karlin and Taylor, 1981].

Let  $X(t)$  denote the state of the process at time  $t = 0, 1, 2, \dots$ , with probability distribution  $p'(t) = \{p^{(0)}(t), \dots, p^{(M)}(t)\}$ . (The prime denotes vector transpose.) Also denote the transition matrix for the process by

$$P = [p_{ij}]_{i,j=0}^M$$

Therefore

$$p'(t) = p'(t-1) \cdot P = p'(0) \cdot P^t.$$

For simplicity, assume the spectral decomposition

$$P^t = \sum_{m=0}^M \lambda_m^t r^{(m)} l^{(m)'}.$$

with eigenvalues  $1 = \lambda_0 > \lambda_1 \geq |\lambda_2| \geq \dots |\lambda_M|$  and left and right eigenvectors  $l^{(m)}$  and  $r^{(m)}$  satisfying

$$l^{(m)'} \cdot P = \lambda_m \cdot l^{(m)'} \quad ; \quad P \cdot r^{(m)} = \lambda_m \cdot r^{(m)}.$$

In particular,

$$l^{(0)'} = [1, 0, 0, \dots] \quad ; \quad r^{(0)} = [1, 1, 1, \dots] = 1.$$

From this,  $p'(t) = l^{(0)'} + o(\lambda_1^t) \rightarrow [1, 0, 0, \dots]$  as  $t \uparrow \infty$ .  
i.e. eventual extinction is certain.

## A2. Transient states

Note that

$$\lambda_0^t r^{(0)} l^{(0)'} = \begin{vmatrix} 1 & 0 & \dots & 0 \\ 1 & 0 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 1 & 0 & \dots & 0 \end{vmatrix}$$

Hence,

$$P^t = \begin{vmatrix} 1 & 0 & \dots & 0 \\ p_{10}(t) & q_{11}(t) & \dots & q_{1M}(t) \\ \vdots & \vdots & \ddots & \vdots \\ p_{M0}(t) & q_{M1}(t) & \dots & q_{MM}(t) \end{vmatrix}$$

where  $q_{ij}(t) = p_{ij}(t)$  is the  $t$ -step transition probability between transient states  $i > 0$  and  $j > 0$ , and

$$\begin{vmatrix} q_{11}(t) & \dots & q_{1M}(t) \\ \vdots & \ddots & \vdots \\ q_{M1}(t) & \dots & q_{MM}(t) \end{vmatrix} = Q^t$$

Here  $Q = [q_{ij}]_1^M = [p_{ij}]_1^M$  is the substochastic matrix of one-step transitions between transient states  
According to the asymptotic estimate in A1, it follows that

$$q_{mn}(t) = \lambda_1^t \cdot r_n^{(1)} \cdot l_n^{(1)} + o(\lambda_2^t), \text{ for } m \text{ and } n > 0.$$

Next, denote survival probability to time  $t$  as

$$S(t) = \text{prob}[X(t) > 0] = \sum_{n=1}^M p_n(t).$$

In particular, if the initial state is  $X(0)=m$ , then

$$S(t|m) = S_m(t) = \sum_{n=1}^M q_{mn}(t) = \lambda_1^t \cdot r_m \sum_{n=1}^M l_n^1 + o(|\lambda_2|^t)$$

Thus  $S_m(t)$  is asymptotically geometrical, with ratio  $\bullet_1$

### A3. Hazard

Let  $T$  be the (random) time of extinction. Then

Survival  $S(t) = \text{prob}[T > t]$ ; and

$$\begin{aligned} \text{Hazard } H_t(t) &= \text{prob}[T \leq t+\tau | T > t] \\ &= 1 - \frac{S(t+\tau)}{S(t)} \end{aligned}$$

For geometrically distributed  $T$ , where  $S(t) = \sigma^t$ , one has  $H_t(t) = 1 - \sigma$ , independent of  $t$ .

For Markov Chains,

$$S_m(t) = \text{prob}[T > t | X(0) = m] = \text{prob}[X(t) > 0 | X(0) = m] \\ = \text{const} \cdot \lambda_1^t + o(|\lambda_2|^t).$$

$$\text{Hence } H_m(t) = (1 - \lambda_1^t) + o(\lambda_2^t) \rightarrow (1 - \lambda_1^t),$$

independent of  $t$  and consistent with the asymptotically geometric character of  $S(t)$ .

#### A4. Path Functionals

Let  $\mathbf{x} = \{X(t); t=0 \text{ to } T-1\}$  be a sample path of the Markov Chain  $C$ . Then any real-valued path functional defines a utility valuation  $U(\mathbf{x})$  for each path. Averaging probabilistically over paths,

$$U^*(C) = E[U(\mathbf{x}) | \mathbf{x} \in C]$$

is a utility valuation for the process  $C$ .

As an important example, let  $U_\tau(\mathbf{x}) = \text{card}[X(\tau)]$ , any scalar measure of population size (cardinality) at a fixed time  $\tau$ . When  $X(0) = m$ ,

$$U_m^* = E_m[\text{card}(X(\tau)) | X(0) = m] = \sum_{n=1}^M \text{card}(X=n) q_{mn}(\tau)$$

Updating provides a sustainability characterization, analogous to hazard:

$$U_m^*(t) = E_m[\text{card } X(t) | X(0) = m, X(t) > 0],$$

i.e. the expected population size,  $t$  years into the future, among populations still extant at time  $t$ . Thus

$$U_m^*(t) = \sum_{n=1}^M \text{card}(X=n) \cdot q_{mn}(t) / \sum_{n=1}^M q_{mn}(t).$$

From the asymptotic estimates of A1, as  $t \uparrow \infty$

$q_{mn}(t)$  approaches  $\lambda_1^t \cdot r_m^{(1)} \cdot l_n^{(1)}$ , and hence

$$U_m^*(t) \rightarrow \lambda_1^t \sum_{n=0}^M \text{card}(X=n) l_n^{(1)} / \sum_{n=1}^M l_n^{(1)},$$

independent of m.

#### A5. Attenuated Survival-Values

Note that

$$E[T] = E \sum_{\tau=0}^{T-1} 1 = \sum_{s=0}^{\infty} \sum_{\tau=0}^{s-1} 1 \cdot \text{prob}[T=s],$$

A generalization leads to calculation of a conditional attenuated survival-value:

$$CV_a(t) = E \left[ \sum_{\tau=t}^{T-1} a^{\tau-t} \mid T > t \right] = \sum_{s=t+1}^{\infty} \sum_{\tau=t}^{s-1} a^{\tau-t} \text{prob}[T=s \mid T > t]$$

$$= \sum_{\tau=t}^{\infty} \sum_{s=\tau+1}^{\infty} a^{\tau-t} \text{prob}[T=s \mid T > t] = \sum_{\tau=t}^{\infty} a^{\tau-t} \text{prob}[T > \tau \mid t > T]$$

$$= \sum_{\tau=t}^{\infty} a^{\tau} S(\tau) / a^t S(t).$$

Thus

$$CV_a(t) = 1 + \sum_{\tau=t+1}^{\infty} a^{\tau} S(\tau) / a^t S(t) = 1 + a \cdot CV_a(t+1) \cdot S(t) / S(t+1). \quad (*)$$

1) For geometric survival probability, with  $S(\tau) = \sigma^{\tau}$ :

$$CV_a(t) = 1/[1-a\sigma],$$

independent of t.

2) For a Markov chain,

$$S_m(\tau) = \text{prob}[T > t + \tau \mid X(t) = m] = \sum_{n=1}^M q_{mn}(\tau) .$$

Hence, with  $S(\tau) = [S_m(\tau)]_1^M$ , and  $CV_\bullet(t) = [CV_\bullet(t) \mid X(t) = m]_1^M$ , one has

$$CV_\bullet(t) = \sum_{i=0}^{\infty} a^i Q^i \mathbf{1} / Q^t \mathbf{1} .$$

In particular, for  $a=1$ ,  $\sum_1 Q^i$  has elements  $\sum_1 q_{mn}(\tau)$ , equal to the expected sojourn time in state  $n$ , given that  $X(0)=m$ .

Also, one may use the iteration formula in (\*) to approximate  $CV(t)$  in simulations. To initiate the iterations, one needs to know  $CV(t_{\max})$  for sufficiently large  $t_{\max}$ . This may be calculated if  $t_{\max}$  is in the asymptotically geometrical period, and one has an estimate of the geometrical ratio  $\alpha$ , or equivalently the asymptotic hazard  $H$ .

#### A6. Cumulative-Value Path Functionals

Next, consider a path utility of the form

$$U(\mathbf{X}) = \sum_{t=0}^{T-1} a^t G[X(t)] ,$$

where  $G(0)=0$ .

With  $\mathbf{x} = \{X(0), X(1), \dots, X(T-1)\}$ , let

$$\mathbf{x}_{\text{trunc}} = \{X(1), X(2), \dots, X(T-1)\} .$$

Then

$$U(\mathbf{X}) = G[X(0)] + a \cdot U(\mathbf{x}_{\text{trunc}}) ,$$

and so, with  $X(0) = m$ , for  $m = 1$  to  $M$ ,



$$U_m^* = G(m) + \sum_{n=1}^M a_{mn} U_n^*.$$

In vector notation, with

$$U^* = [U_m^*]_1^M, \text{ and } G = [G(m)]_1^M,$$

these equations are expressed in matrix form as

$$U^* = a Q U^* + G, \text{ i.e. } [I - aQ] U^* = G.$$

Inverting,

$$U^* = [I - aQ]^{-1} G = [I + aQ + a^2 Q^2 + \dots] G.$$

This derivation may be generalized to allow  $G(0) \neq 0$  and a terminal  $g(T-1)$ .

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```

program NewOwl12: {1,000 year survival and expected population}
  (30,000 replicates!)      (Vary initial conditions)
($R-)
($N+)
const
  singsurv=7E-1; pairsurv=94E-2; pairmort=6E-2; juvsurv=6E-1; sites=255;
  totsites=1000; replicates=30000; search=26; DecadeSpan=200;
type
  vectr=array[0..200] of word;
  matr=array[0..200, 1..4] of longint;  (Note: Change range of vectr,)
  matsx=array[0..200,1..4] of single;  (matrx, matsx with DecadeSpan)
  (or initial cond'n options)
var
  j, N, NN, T, Ct,Ct1, Ct2, Tm, S, YearSpan: word;      M:longint;
  indicator, fecundity, avsites, disperse, mate, adjust,
  singles, pairs, juveniles, nxtsingles, nxtpairs, usedsites :single;
  Yrs: vectr;
  one, two, InitOccup: array[1..4] of single;
  survive, popul: matr; P, CO: matsx;   owlfile: text;
function xTOy(X,Y:extended):extended;
begin
  xTOy:=exp(y*ln(x));
end;
begin {program OwlExtin4}
  randomize;
  YearSpan:=10*DecadeSpan;
  for N:=1 to 4 do begin
    InitOccup[N]:=10+10*N;
    one[N]:=0.002*InitOccup[N]*Sites; two[N]:=0.008*InitOccup[N]*sites;
    for j:=0 to DecadeSpan do begin
      survive[j,N]:=0; popul[j,N]:=0;  (initialize)
      Yrs[j]:=10*j;
    end; {j-loop}
  for M:=1 to replicates do begin      (the Mth replicate)
    (initialize: generation count, population)
    S:= 0;  T:= 0;  singles:=one[N]; pairs:=two[N];
    while (pairs>=1) and (T<=YearSpan) do begin  (run replicate)
      indicator :=random;  (set random fecundity)
      if (indicator<8E-1) then fecundity:=2E-1 else fecundity:=7E-1;

```

```

juveniles:=fecundity*pairs;
avsites:=sites-pairs-singles;
disperse:=1 - xTOy((1-avsites/totsites),search);
mate:=1 - xTOy((1-singles/totsites), 2*search);

(Time step)
nxtsingles:=juveniles*juvsurv*disperse +
(singles*singsurv+pairs*pairmort)*(1-mate);
nxtpairs:=(1-2*pairmort)*pairs + singsurv*mate*singles;
usedsites:=nxtsingles+nxtpairs;
if (usedsites>sites) then adjust:=sites/usedsites
else adjust:=1;
singles:=nxtsingles*adjust; pairs:=nxtpairs*adjust;

(periodic record)
if (T mod 10 = 0) then begin
S:= T div 10;
survive[S,N]:=survive[S,N] + 1;
popul[S,N]:=popul[S,N] + round(singles + pairs);
end;
T:=succ(T);
end; (T-loop)
end; (M-loop)
end; (N-loop)

for Ct2:=1 to 4 do
for Ct1:= 0 to DecadeSpan do begin;
P[Ct1, Ct2]:= survive[Ct1, Ct2] / replicates;
if survive[Ct1, Ct2]> 0
then CO[Ct1, Ct2]:=
popul[Ct1,Ct2] / (survive[Ct1,Ct2]*sites)
else CO[Ct1, Ct2]:=0;
end; (Ct1-loop)

(create file)
assign(OwlFile, 'A:\NewOwl12.Dat');
rewrite(OwlFile);
writeln(OwlFile,
'Lapsed time vs. survi prob and cond _I occup: for 25.5% Old Growth:');
write(OwlFile, '%InitOccup');
for NN:=1 to 4 do
write(OwlFile, InitOccup[NN]:10:1);
write(OwlFile, ' ** ');
for NN:=1 to 4 do
write(OwlFile, InitOccup[NN]:10:1);
writeln(OwlFile);

```

```

for Ct:=0 to DecadeSpan do begin
  write(OwlFile, Yrs[Ct]:10);
  for NN:=1 to 4 do
    write(OwlFile, P[Ct,NN]:10:5);
  write(OwlFile, '  ');
  for NN:=1 to 4 do
    write(OwlFile, CO[Ct,NN]:10:5);
  writeln(OwlFile);
end; (Ct-loop)
close(OwlFile);

end.

```

# DOCUMENTATION FOR FIGURES (Parameter Values)

Default Values: As shown in program, except usually 20% of occupied sites are singles, 80% are pairs.

Fig.1: 40 sites searched

Fig.2: Sites searched: 26 or 40;

LoFecun: .25 (prob .8), .5 (prob .2), mean .3  
 HiFecun: .20 .7 mean .3

Fig.3: InitOccup: 75%

Fig.4-6: OldGrowth: 25.5%

Fig.7: OldGrowth 20%, InitOccup 50%

Fecundity (all with mean 0.3):

Level 1) 0.1 (prob .8), 1.1 (prob .2),

2) 0.2 0.7

3) 0.22 0.62

4) 0.25 0.5

Fig.8-12, 15: Lo Old Growth 20%, Hi Old Growth 25.5%

LoFecun: .2 (prob .8), .7 (prob .2), mean .30

HiFecun: .11 1.21 mean .33

Fig.13-14: Fecundity levels:

Level 1) 0.11 (prob .8), 1.21 (prob .2) mean .330

2) 0.216 0.756 .324

3) 0.2266 0.6386 .309

4) 0.25 0.5 .300

Fig.16: % Old Growth 25.5%; Fecundity: .2 (prob .8); .7 (prob .2);

# 250 YEAR SURVIVAL

alternative biological and environmental assumptions

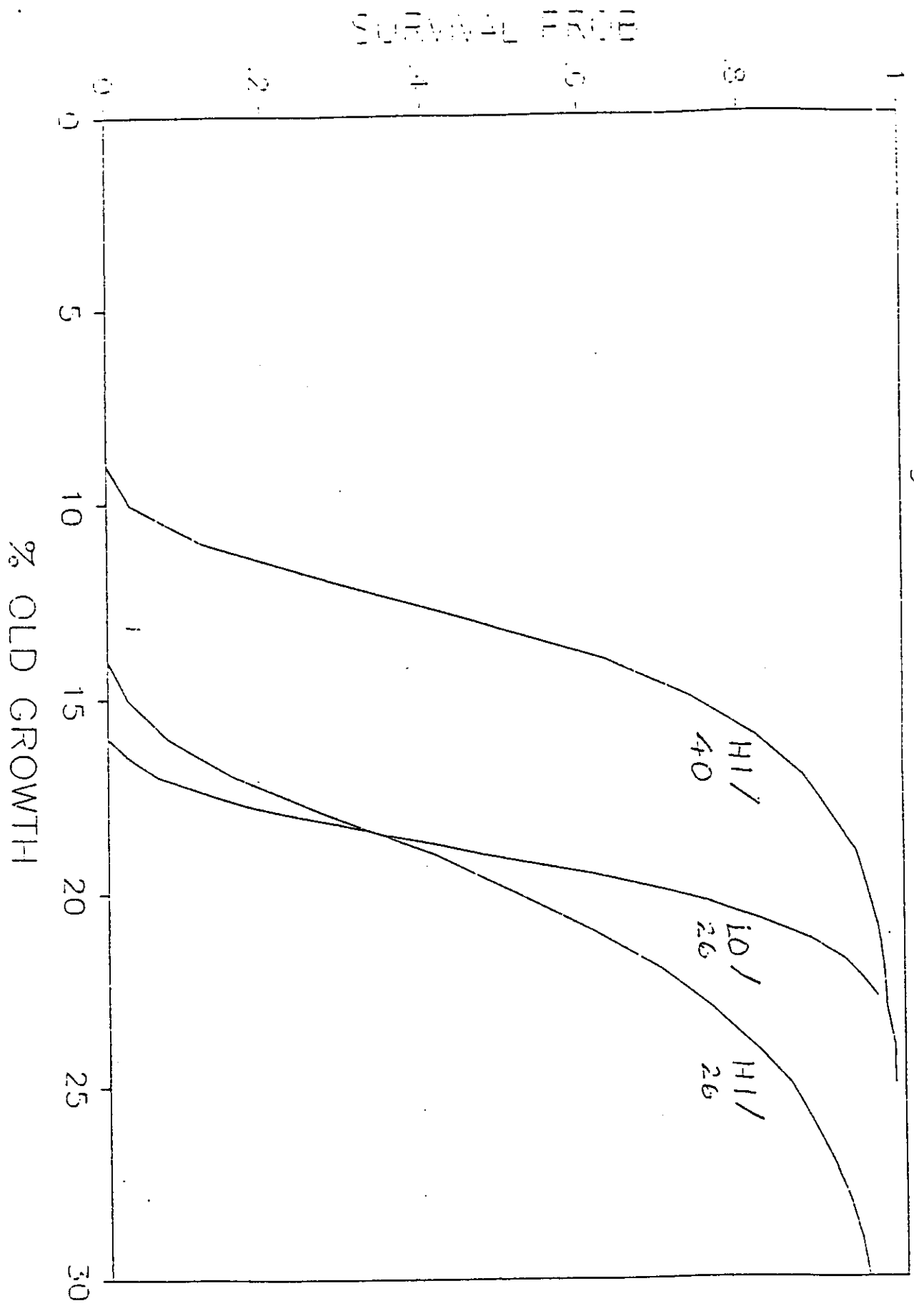
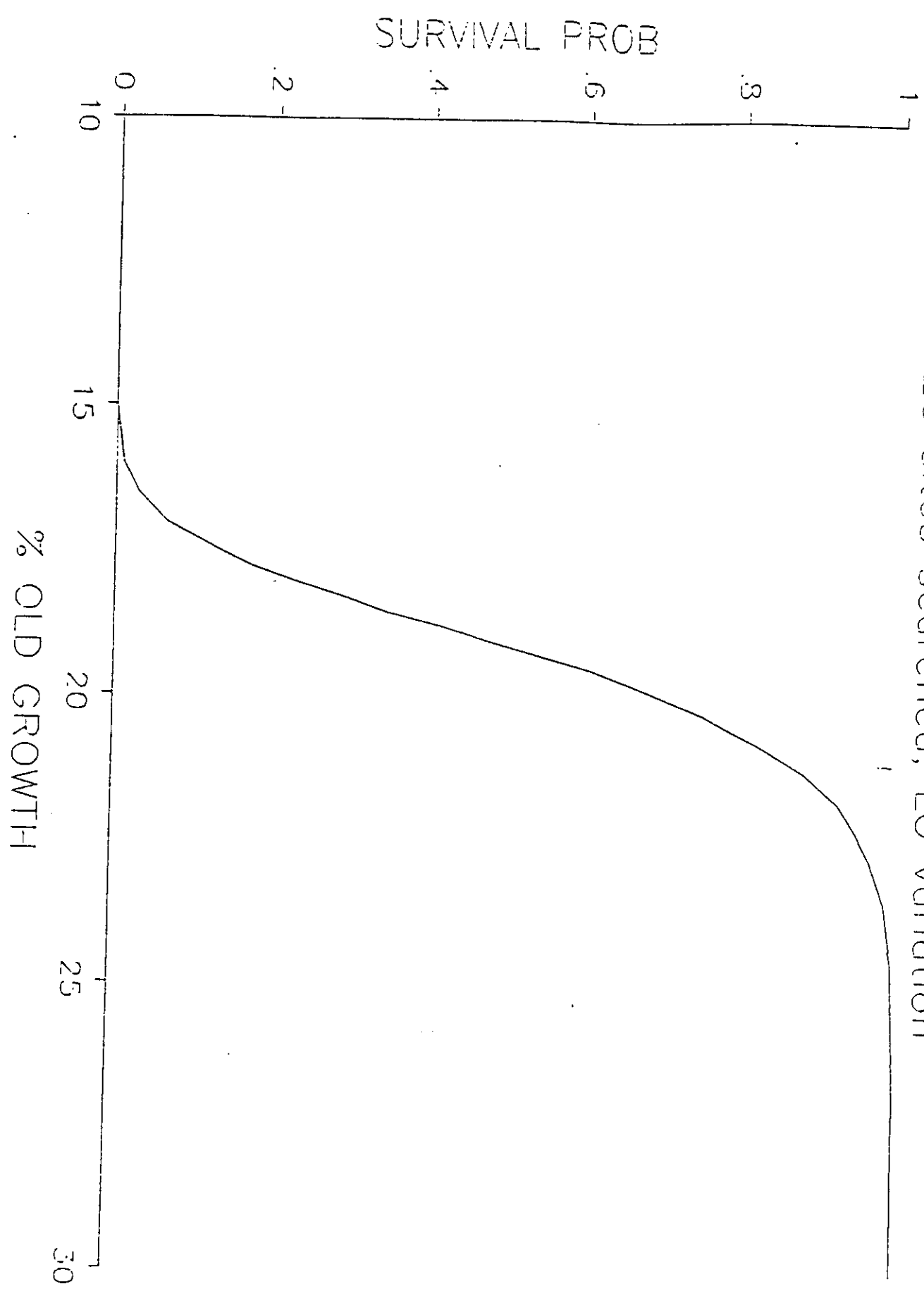


Fig. 2

# 250 YEAR SURVIVAL 26 sites searched; LO variation



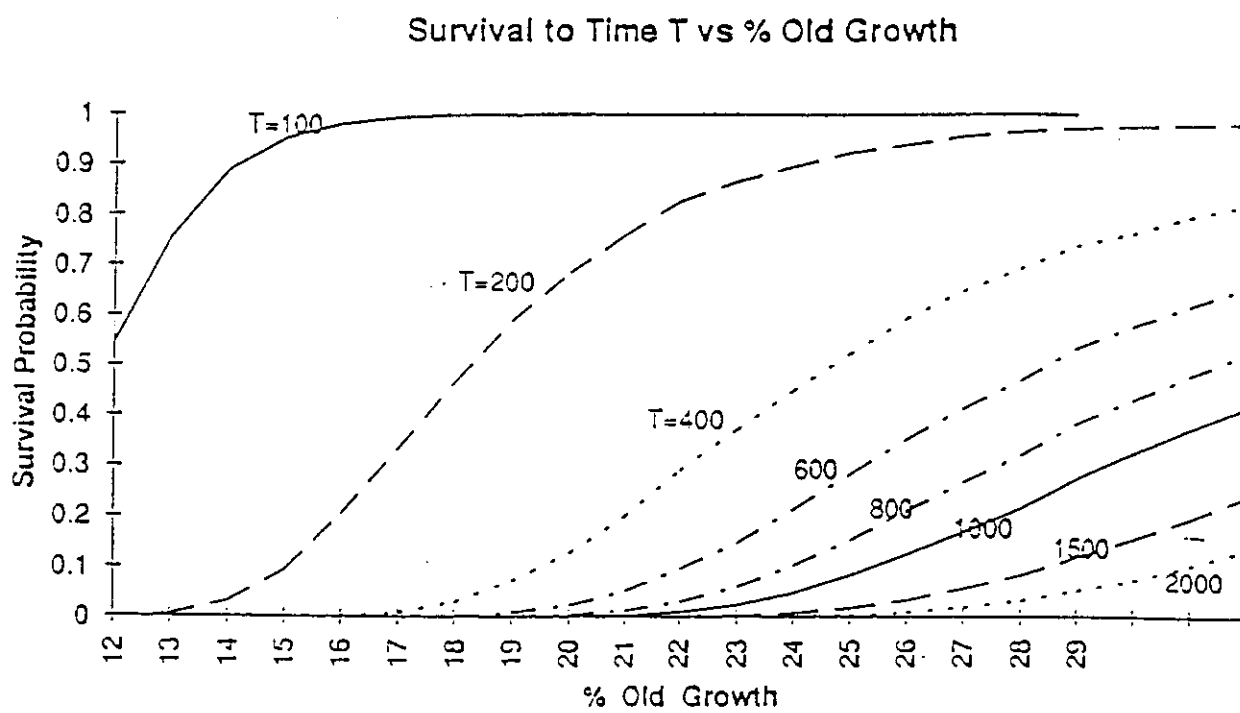


fig. 3



Survival Probability vs Time For Various Levels of Initial Occupancy

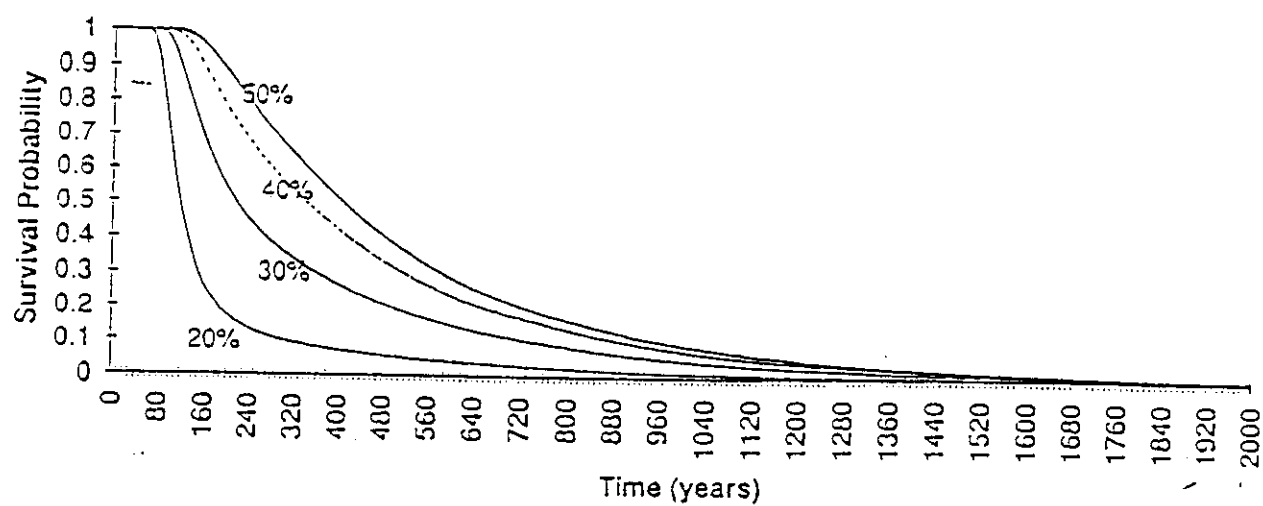


fig. 4

250-year Hazard vs Time, for Various Levels of Initial Occupancy

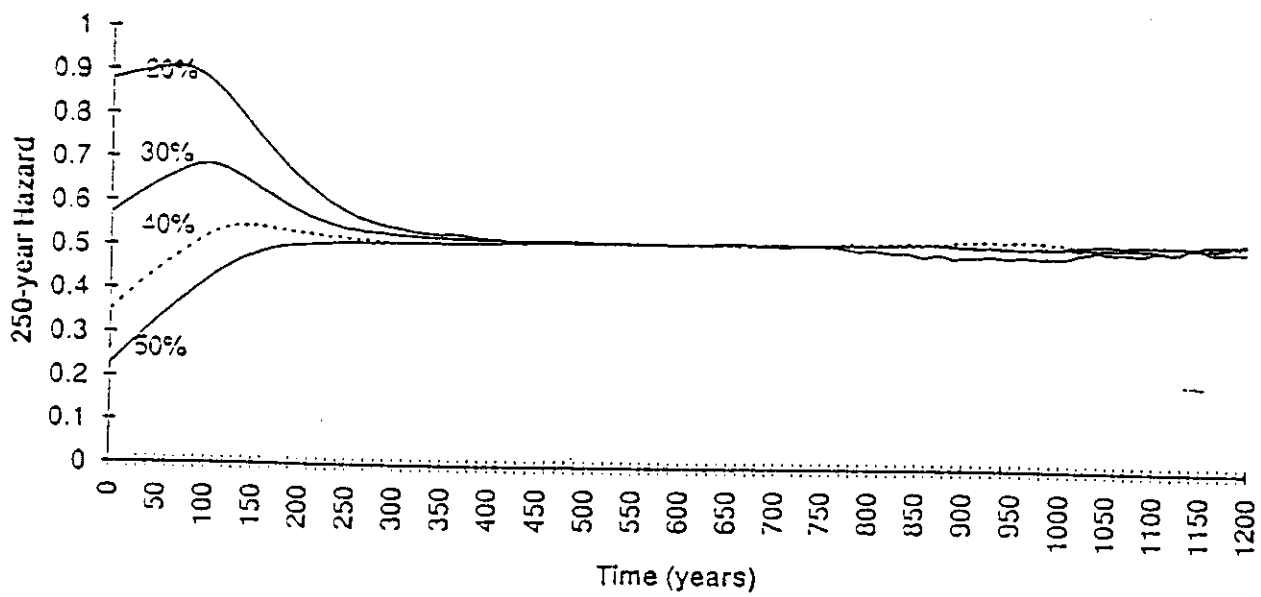


fig. 5

100-year Hazard vs Time for Various Values of Initial Occupancy

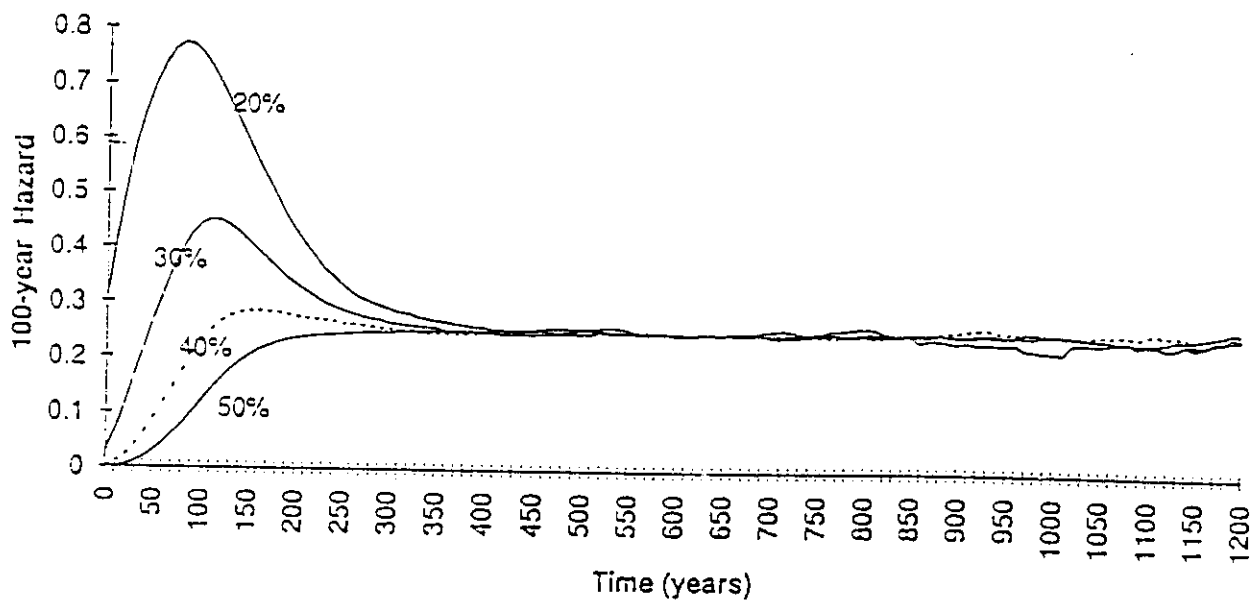


fig. 6

100-yr Hazard, for various stochasticities

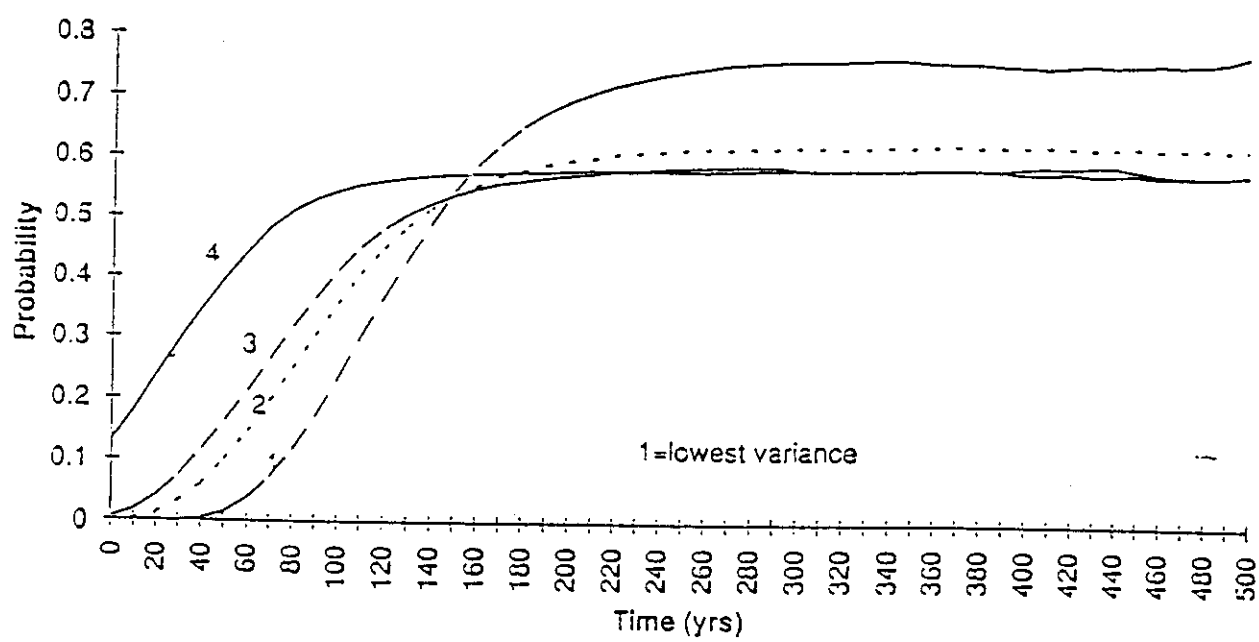


fig. 7

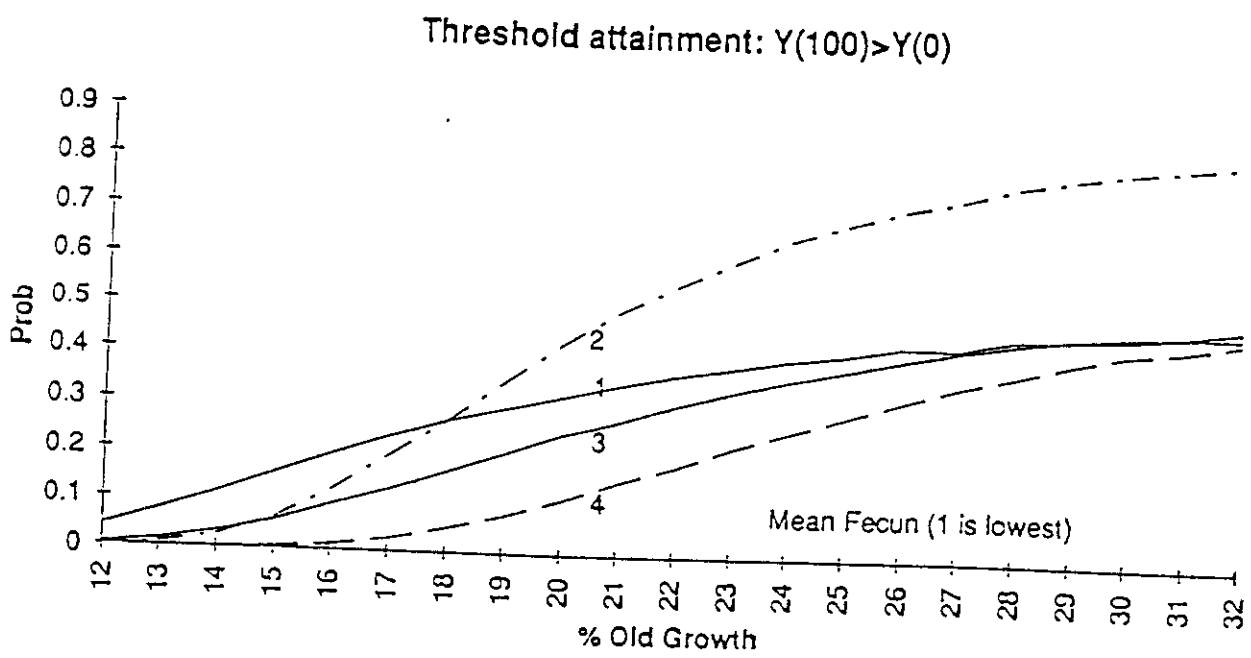


fig. 8

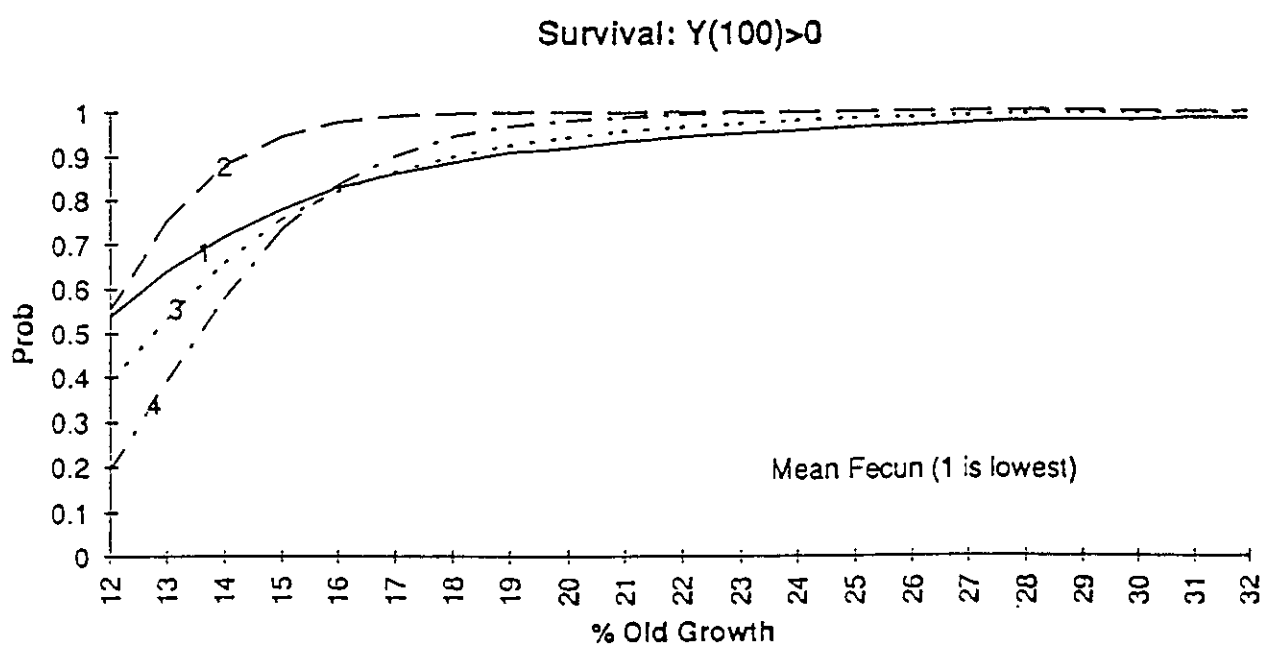


fig. 9

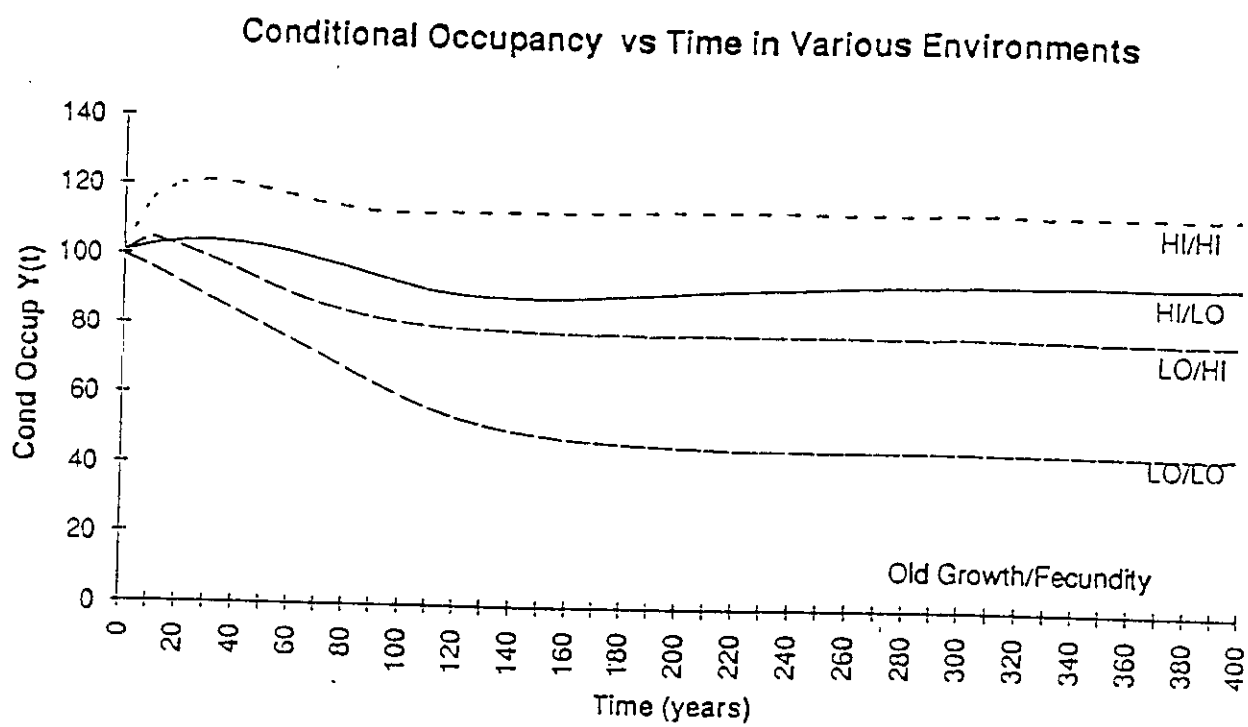


fig. 10

### Asymptotic Cond'nl Prob Density of Occupancy

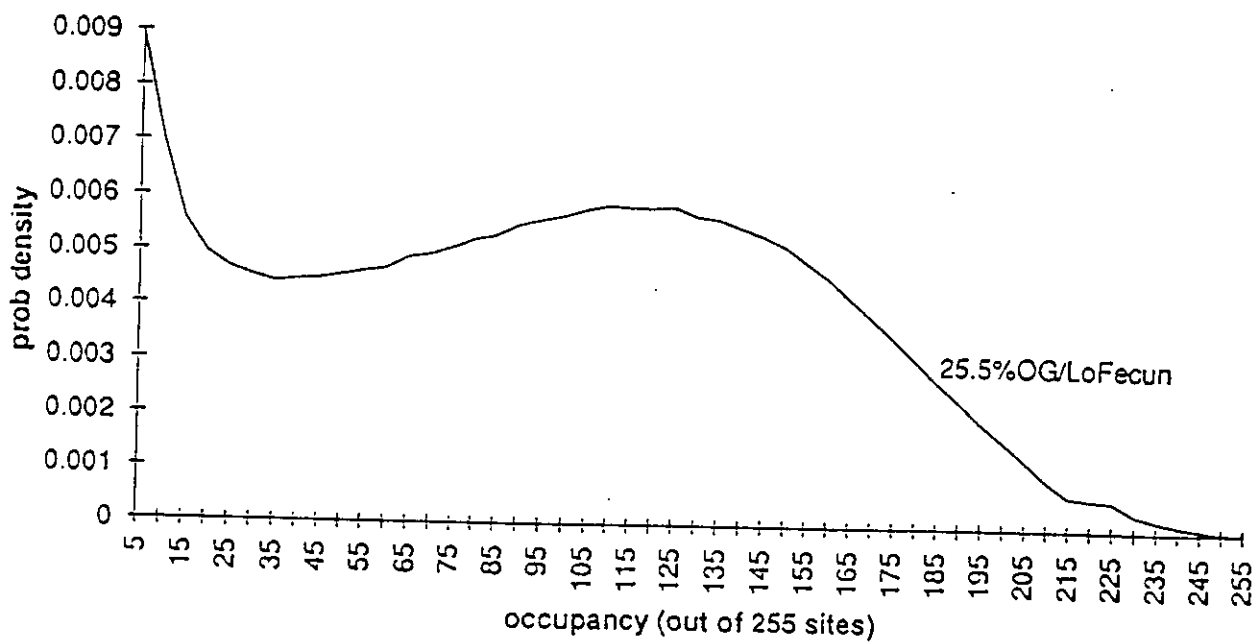


fig. 11



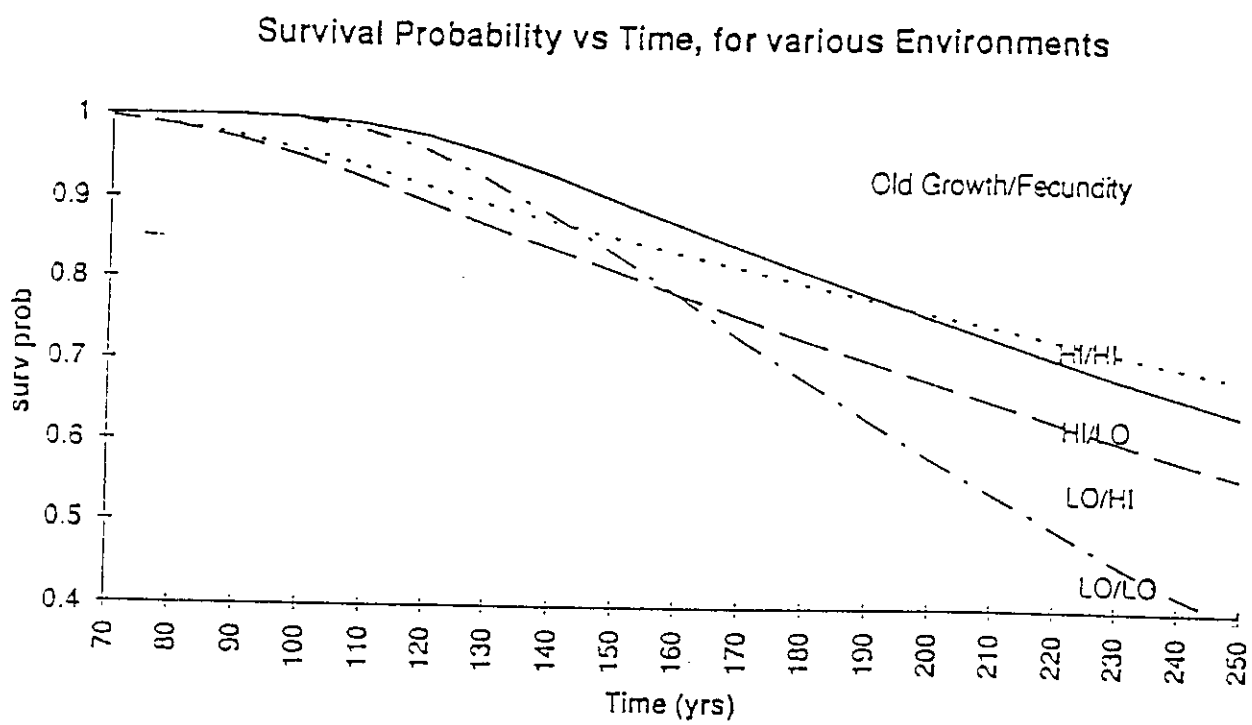


fig. 12

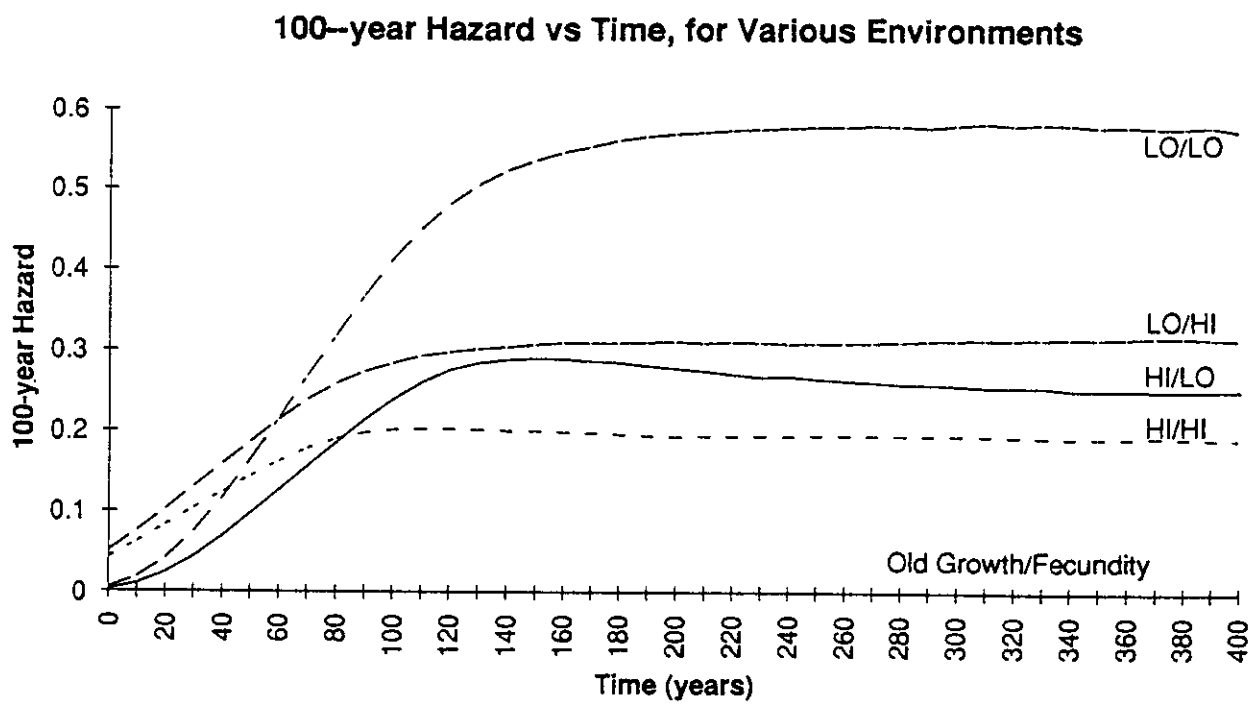


fig. 13

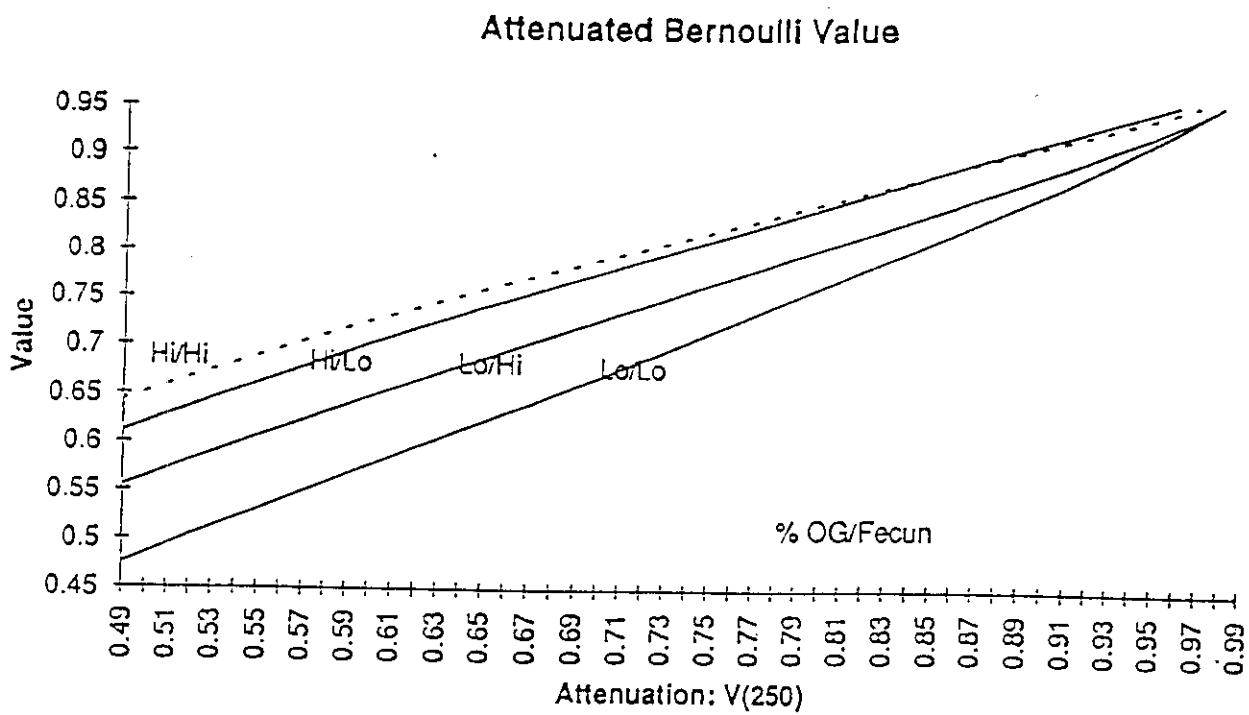


fig. 14

Conditional Attenuated Value, for  $V(250)=.9$

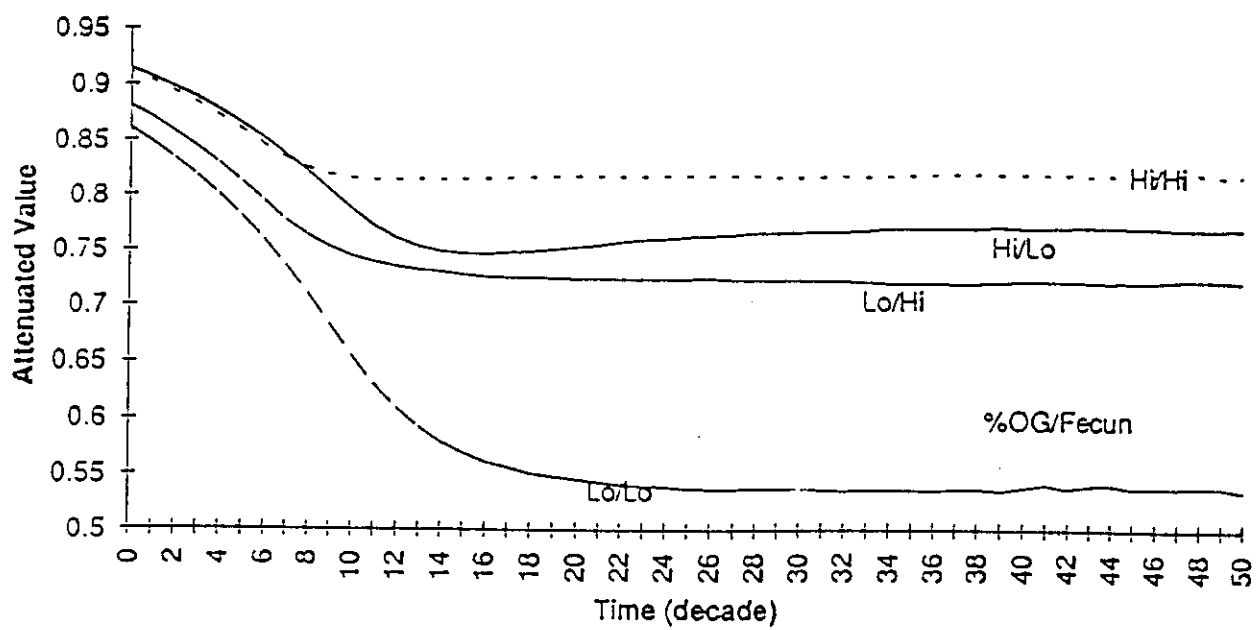


fig. 15

Conditional Attenuated Value, for  $V(250)=.5$

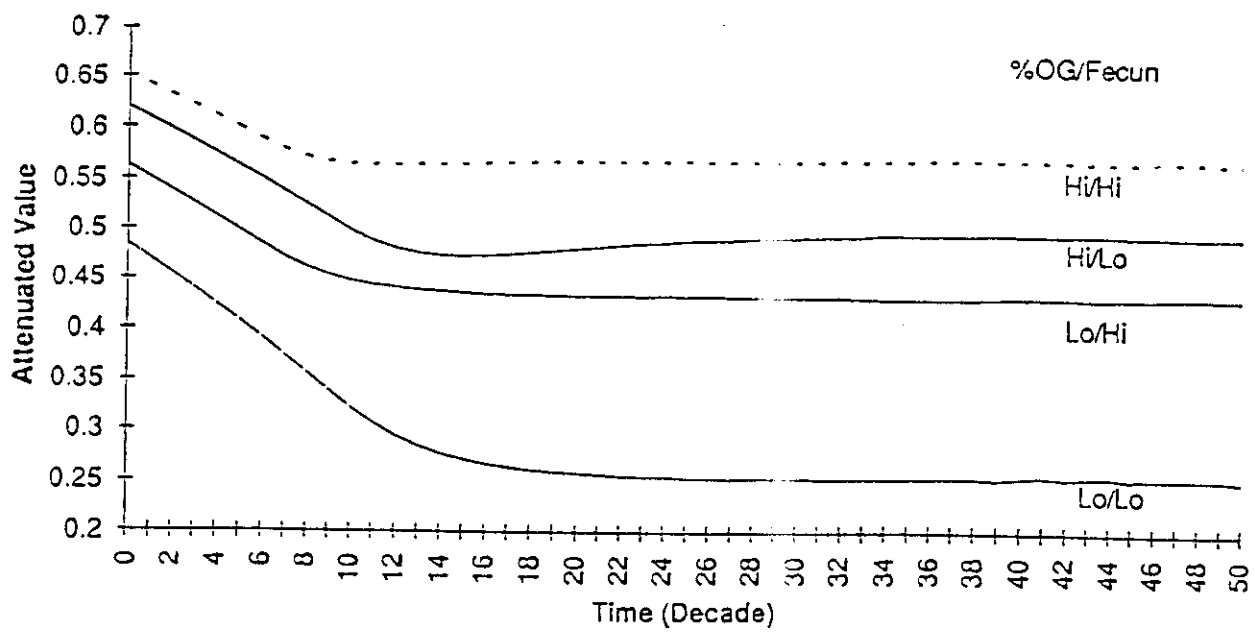


fig. 16

VIABILITY ANALYSIS OF ENDANGERED SPECIES:  
A DECISION-THEORETIC PERSPECTIVE

SUPPLEMENTARY REMARKS: PROBING THE ASYMPTOTIC TEMPORAL REGIME

1. In the Decision Theory paper it is argued that the asymptotic behavior of a population, after initial transients have died out, needs to be explored whenever a current decision's ramifications persist into that asymptotic era, and especially if such impacts cannot be corrected for in the interim. For the spotted owl, this may apply to landscape management decisions, e.g. a decision to clearcut a particular tract of mature or maturing forest.

This note addresses some aspects of the technical problem of "seeing into" the asymptotic era through computer simulation of a model. In carrying out the simulations for the spatially-homogeneous owl model, I found it necessary to carry out at least 30,000 simulation runs to sample each data point. The purpose of this note is to illustrate why this was so, and to back up the illustrations with some simple theoretical calculations.

Figure A illustrates the difficulty. This is the same graph as in fig.6 of the paper, except that it is run out to 3000 years. In order to obtain unambiguous results, each graph shown is obtained from 100,000 simulation runs.

However, hazard is a conditional probability, hence an individual data point on the graph calculates the hazard at a particular time  $t$  by averaging over only those computer runs for which populations have not yet gone extinct at  $t$ . Furthermore, the number of these drops off geometrically over time, as can be seen in fig.4 of the paper. From the simulation data, an initial run size of 10,000 will drop off over time as follows:

Initial Occupancy:	20%	30%	40%	50%
Original run size:	10,000	10,000	10,000	10,000
After 400 years;	701	2,636	4,161	5,056
After 500 years	520	1,972	3,131	3,794
After 600 years	387	1,461	2,350	2,854
After 800 years	219	819	1,327	1,606
After 1000 years	123	461	739	901

Thus an initially large set of simulation runs quickly becomes much smaller and, as it does, sampling errors begin to grow and distort our estimates of statistical quantities. In figure A,

for example, with an initial run size of 100,000, sampling errors become noticeable around year 1500, and by the year 2000 they severely limit our ability to observe the asymptotically constant level of hazard.

Thus there is a window in time within which we can observe the asymptotic regime. It begins when the leading non-unit eigenvalue of the transition probability matrix finally dominates over the others, and ends when sampling errors become excessive.

If one cuts down significantly on the number of sampling runs, from the 100,000 runs used in fig. A, then sampling error will become serious at an earlier time, and the window of observability will narrow.

2. Figures B, C, and D show these effects as they apply to observing asymptotic hazard, in the case where the model is run at 4 different levels of environmental stochasticity. Here, level 1 has the highest variance, old growth level is 25.5%, and the figures shown summarize 100,000 runs. Since initial occupancy is 80%, hazard rises monotonically to its asymptotic level.

Note that asymptotic hazard increases as environmental stochasticity increases. Note also that sampling error breaks up the steady-state asymptotic hazard at different times depending on stochasticity level, with break-up occurring earlier as stochasticity increases. This is the result of two reinforcing effects: As stochasticity increases, populations go extinct at a more rapid rate, and also the variation increases in the sampled population runs.

As asserted above, the window of observability of the asymptotic hazard narrows as the run size decreases. The location of both onset and break-up are subjective, but one may estimate that:

i) For level 4, the asymptotic era begins about at 420 years, with break-up seeming to occur at

- \*2500 years when run size is 100,000;
- \*1710 years when run size is 30,000;
- \*835 yrs. when run size is 10,000.

ii) For levels 2 or 3, the asymptotic era seems to begin at 300 years; with breakup occurring about at

- \*1300 years when run size is 100,000;
- \*900 years when run size is 30,000;
- \*500 years when run size is 10,000;

iii) For stochastic level 1, the asymptotic window begins at approximately 180 years and sampling-error break-up begins at approximately

- \*340 years, when the run size is 100,000;
- \*165 years--before the asymptotic era--for run size 30,000;

3. Of course there are other aspects of the asymptotic regime, in addition to hazard, that may be important in devising management strategies. One is the asymptotic population size, which we measured as conditional occupancy. (In a spatially-inhomogeneous model, spatial population distribution also will be important.)

In the October version, fig. 10 shows expected conditional occupancy, and fig. 11 shows its distribution function. (These are figs. 15 and 16 in the earlier versions). What is important at the moment is the very small probability densities involved in fig. 11: The Owl population sizes are grouped into 26 categories, with probabilities mostly around .05. It follows that to accurately graph such a curve, one needs to worry about relative errors (i.e. fractional errors) rather than additive errors.

Survival  $p$  to a fixed horizon is simply a Binomial random variable. Consequently, for a sample of size  $N$ , the relative error  $E/P$  in a sample estimate  $P$  of  $p$ , is

$$E/P = Z_{\alpha} \sqrt{(1-P)/P} \sqrt{1/N},$$

with confidence  $1-\alpha$ . Here  $Z_{\alpha} = 1.96$  or  $2.575$  resp, when  $\alpha = .05$  or  $.01$ . (Using the Gaussian normal approximation.)

Thus, with 95% confidence,  $|E/P|$  will not exceed the quantity in the body of the following table:

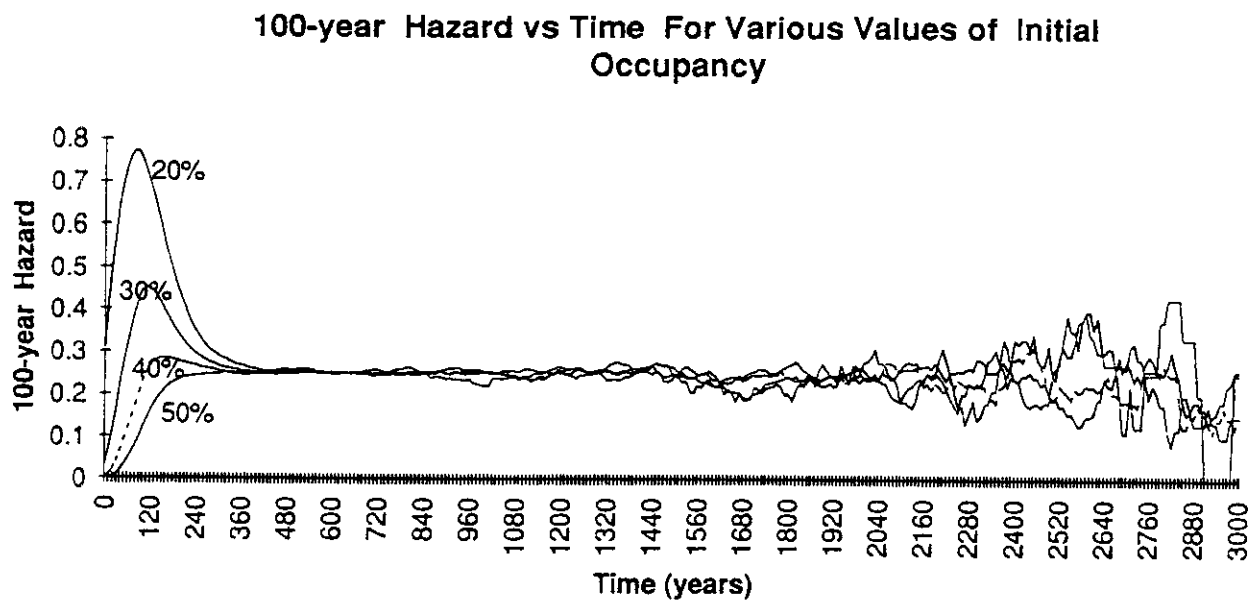
N=	1,000	10,000,	100,000
P= .5	.078	.020	.006
P= .1	.186	.059	.019
P= .01	.616	.195	.062

With 99% confidence,

N=	1,000	10,000	100,000
P= .5	.081	.026	.008
P= .1	.244	.077	.025
P= .01	.810	.256	.082

It seems reasonable to try to keep the relative error smaller than .05 in rough graphing, and even smaller for examining more delicate issues. Note that  $N$  is the residual number of runs not yet extinct by the asymptotic era, not the initial number at  $t=0$ .



*Fig A.*

## Hazard at Venus Stochasticities

1 = highest stochasticity

4 = lowest "

100 yr hazard

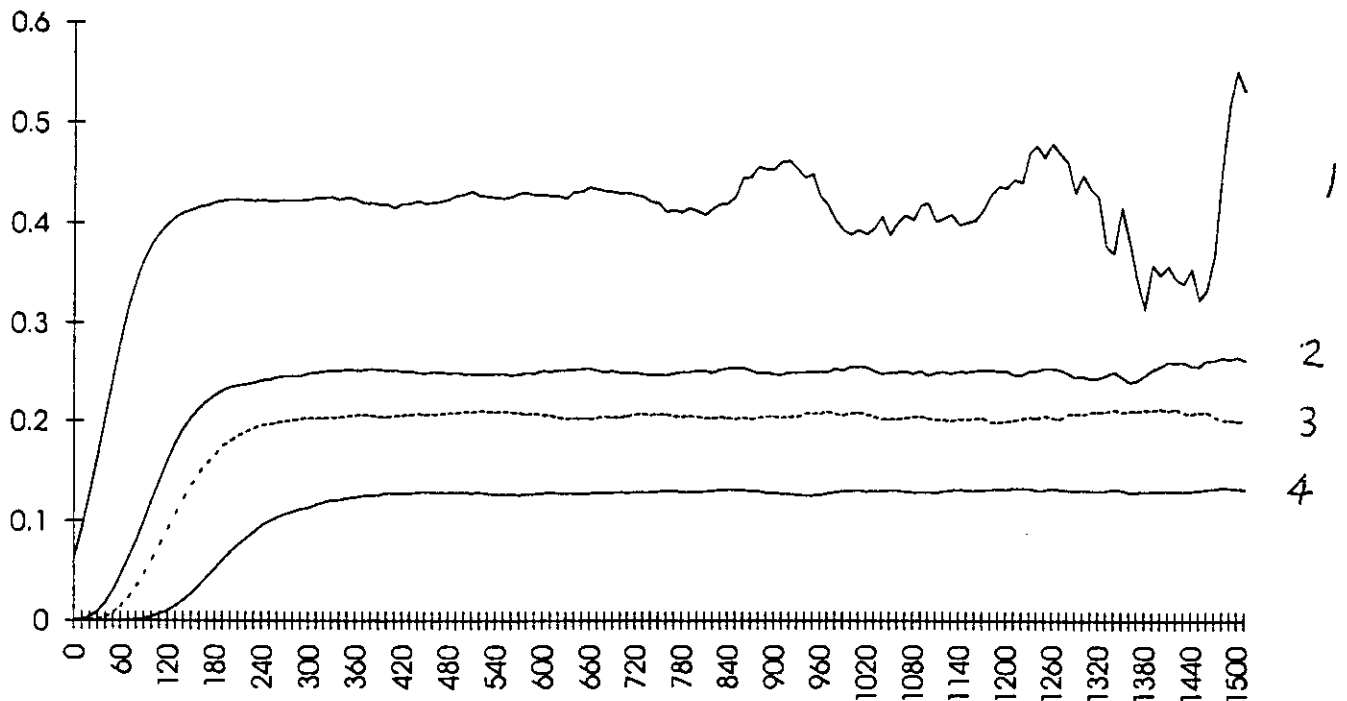


Fig B.

# Hazard at Various Stages

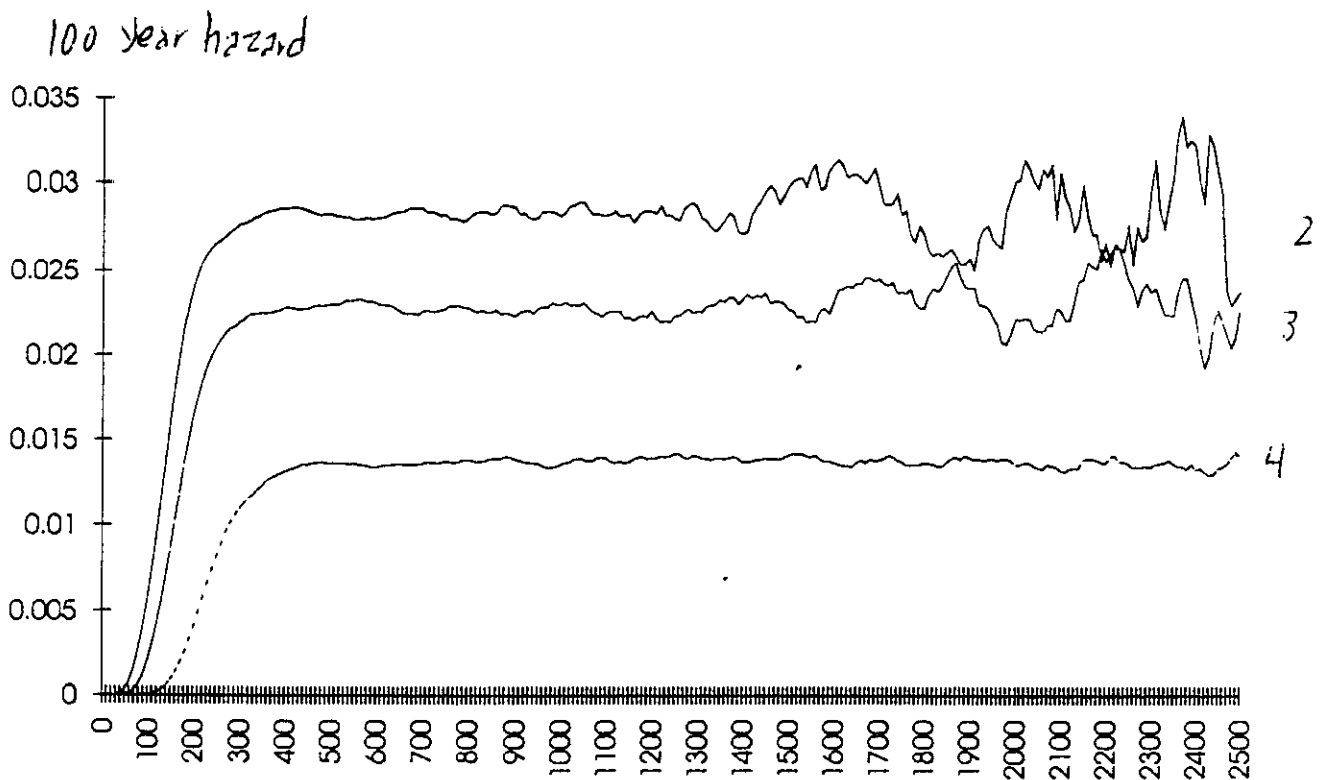


Fig C

# Hazard at Low Stochasticity

100 yr Hazard

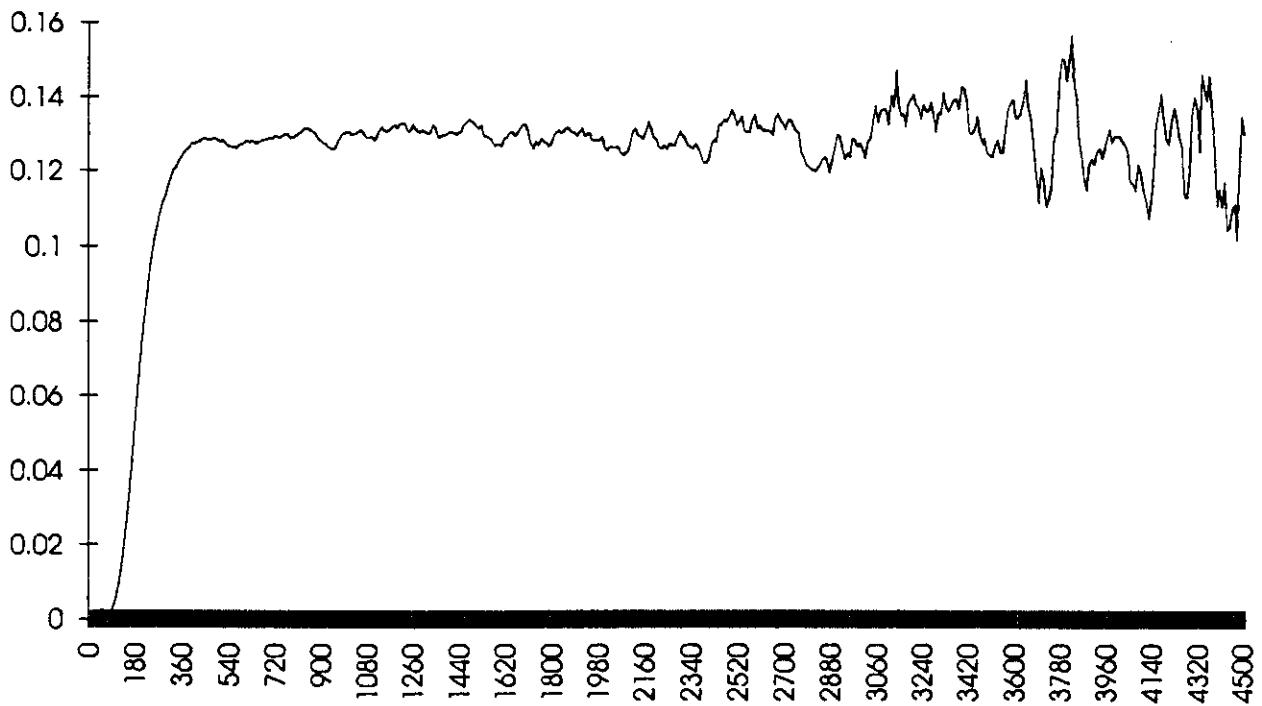


Fig D.