Taxonomic Survivorship Curves[1]

Leigh Van Valen
Department of Biology
University of Chicago
1103 East 57th Street
Chicago, Illinois 60637

Abstract: I give methods for the treatment of data from living and extinct taxa with respect to taxonomic survivorship curves, and comment on some of the aspects of deviations from loglinearity by such curves.

*   *   *

In 1973 I gave evidence that for all, or almost all, ecologically homogeneous taxa for which data were available, the probability of extinction of subtaxa of any rank has been stochastically constant within observed error. The characteristic probability varies among taxa and categories. Raup (1975) called this result Van Valen's Law. (The name is unfortunate because in 1976 I proposed a more basic law, that natural selection at any single level or time scale always maximizes regulatory energy. Expansive energy and control of trophic energy approximate regulatory energy.)

Critiques of certain aspects of the Law of Constant Extinction have appeared (Raup, 1975, 1978; Sepkoski, 1975; Salthe, 1975; Foin, Valentine, and Ayala, 1975). I have answered some of these (Van Valen, 1975, 1976a), but more detailed analyses of these and other points remain unpublished. The only point I find both valid and relevant is Sepkoski's implicit demonstration that my threshold for rejecting poor data was a little too lenient.

The present paper bears implicitly on some of the above matters and on other recent work by several people. An adequate explicit treatment must involve several other aspects; for now I give information only.

The theory of taxonomic survivorship curves is more complicated than it may seem at first glance. There are several cryptic biases which are sometimes important. I give here a general treatment of certain analytical and statistical aspects of the theory. The analysis is somewhat intricate, and wrong turns are easy to make. I therefore give the analysis in an extended form rather than assuming knowledge of what is known. The analysis is applicable also to other linear survivorship curves with similiar problems of estimation, as can happen in ecology.

LIVING AND EXTINCT TAXA

Nature of the population. It is necessary to pay strict attention to the nature of the statistical population whose survival is being estimated. This population has been in existence for a finite period of time. If there is a nonzero probability that a taxon can survive longer than this interval, or if a stable age distribution of the taxa has not yet been reached, a bias is introduced into the usual analysis of survivorship curves. This bias decreases as the interval increases, but is important when the half-life of a random taxon is a moderate fraction of the total interval.

*   *   *

[1] Contribution No. 2, Lothlorien Laboratory of Evolutionary Biology

Consider pelecypod families. The population is all pelecypod families that have ever existed. (It is also possible to regard the population as infinite, defined by those common properties or variables of pelecypod families that happen to be of immediate interest. The distinction is unimportant here, and I have used the second alternative because its analysis is easier. My terms will usually reflect the discrete case, however; e.g., I use "probability" instead of "probability density" because it is more familiar.) It is crucial that the population comprises all those families which originated in some finite interval of time. What we want to know is the pattern of survivorship of this population. Survival will extend far beyond the present, given conditions like those of the past, but families originating in the future, during this period of survival, are not part of the population under consideration. Our incomplete sample from this population contains some families which are still alive and others which have already become extinct.

Conceptually, we place the origin of all families at one point in time (which we may call survivorship time) and follow their survival. We know, or rather can estimate more or less adequately, the duration of those families that have become extinct. However, for families that are still alive there is a difficulty. Their observed durations are less than their total durations, because they will survive some unknown intervals into the future.

We want to estimate their total duration. A first guess might be to give each living family the same probability of extinction per unit time as those families which have already become extinct. But this is improper, because the data are biased. The surviving taxa of a group have a longer expected observed duration in any finite interval than do the extinct ones (Van Valen, 1973a, note 5). This bias occurs because the longer the total survival of a taxon, the greater the probability of its being intersected by a random (random in real geological time) time-slice like the present.

One might think (Raup, 1975) that because the cumulative distribution of durations of extinct taxa and the observed (noncumulative) distribution of ages of living taxa each estimate a l_x distribution, one can simply combine these distributions to estimate optimally the life-table parameters. Unfortunately such a method is biased. The distribution of the total includes the total durations of all the taxa, including the parts remaining in the future. This method simply deletes from the total distribution the parts not yet reached. The latter are not a random sample of the total, and this bias can be important. For a taxon of any total duration, the average position for a random time-slice to cut it is at the middle. Because longer-lived taxa are the most likely to be cut at all, the distribution of the parts deleted is biased in the direction of long-lived taxa. And as noted earlier, one can't simply double the observed ages of taxa now alive, because there is a different bias.

Another guess might be to double the observed age of each living taxon, because a random time-slice will cut the total duration of a taxon in half, on the average. However, there is a bias in ascertainment here. We know the ages to the present, not the total durations. Because taxa of long total duration are rarer than those of short total duration, a high observed age is more likely to extend into the second half of a moderately long taxon than to be confined to the first half of a very long taxon. Doubling this age will overestimate the expected total duration unless there are bradytelic taxa present.

TAXONOMIC SURVIVORSHIP CURVES

A fourth possible method (S.M. Stanley, personal communication) is to multiply the number of living taxa in each age-group by the ratio of the longest observed age to the age of the given age group. However, this also is biased. Even at equilibrium some taxa which will eventually have long survivals will be cut by the time-plane early and so will appear short-lived, while the reverse case can't happen. The method would work if we used the total survivals, not the survivals to the present, but if we had that information we could use the data directly.

My analysis will assume that the rates of origination and extinction, in the sense of the probability of such events per existing taxon, have been constant throughout the interval and equal to each other. The known falsity of this assumption (Van Valen, 1973a) is more important for the case of living taxa than for the total sample or for extinct taxa. The special circumstances in an interval of real time, which is all we have for living taxa, are more nearly averaged out in the survivorship time of the other two cases, where the common properties of the ecological group under consideration have a greater effect. Extinction rates vary over time but can nevertheless approximate a distribution which is stationary over time. Such a distribution reflects the ecological interactions of the higher taxon considered.

The Total Population. By the Law of Constant Extinction, the probability of a taxon becoming extinct is constant in survivorship time. For the purposes of this analysis I will ignore all second-order irregularities in this constancy. The analysis deals with survivorship time (age) unless I state otherwise.

Initially, at time $y = 0$, there is a cohort consisting of N_0 taxa. At some later time $y = x$, there are only N_x taxa. The proportionate survival to time x is called

$$\ell_x \equiv \frac{N_x}{N_0} . \tag{1}$$

In the case of constant probability of extinction,

$$\ell_x = e^{-ax}, \tag{2}$$

where a is a constant expressing the instantaneous force of mortality or extinction (the decay constant for radioactive decay), m is the probability of extinction per unit time,

$$a = -\ln(1 - m) = \frac{-\ln \ell_x}{x}, \tag{3}$$

e is the base of natural logarithms, and ln designates the operation of taking natural logarithms. For convenience, the probability of survival per unit time

$$s \equiv 1 - m = e^{-a}. \tag{4}$$

The proportion of N_0 that die at time x is called d_x. In general,

$$\ell_x = \int_x^\infty d_y \, dy .$$

(5)

For constant extinction,

$$d_x = a e^{-ax} ,$$

(6)

$$\ell_x = s^x ,$$

(7)

and, as a discrete approximation,

$$d_x = m s^x .$$

(8)

If we plot l_x against t (survivorship against time), using a logarithmic ordinate, the curve will be a straight line with slope $-a$ if the logs are to the base e, and $-a/(\ln 10) = -0.4343a$ if the logs are to the base 10. The proportion Q of the survivors at any time, that are lost in some interval of time w, is

$$Q = 1 - e^{-aw} .$$

(9)

Conversely,

$$w = \frac{-\ln(1-Q)}{a} .$$

(10)

And specifically, for the half-life h, $Q = 1/2$ and

$$h = \frac{-\ln\left(\frac{1}{2}\right)}{a} = \frac{0.693}{a} .$$

(11)

The half-life is a median and the life expectancy is a mean. In general, the life expectancy E_x at time x is

$$E_x = \frac{\int_x^\infty \ell_y \, dy}{\ell_x} .$$

(12)

TAXONOMIC SURVIVORSHIP CURVES

For constant extinction, $\underline{E_x}$ is constant for all $\underline{x}$:

$$E_x = \frac{1}{a}.$$

(13)

Note that

$$E_x = 1.443h.$$

(14)

<u>Extinct Taxa</u>. To quantify the bias in ascertainment between living and extinct taxa, we must examine the two cases separately. That for extinct taxa is simpler.

Consider an interval in real time from $\underline{t}$ million years ago to the present. A taxon arises at some random time in the interval, and has some duration $\underline{x}$ before its extinction. Given this random origination, the probability that it will become extinct before the present is

$$p_e(x) = \begin{cases} \left(1 - \frac{x}{t}\right), & x \le t \\ 0, & \text{otherwise}. \end{cases}$$

(15)

In survivorship time, this is the probability that the random time-slice of the present fails to hit the taxon. For the taxon to be extinct, $\underline{x}$ must be less than $\underline{t}$. In the total population of taxa, living and extinct, the proportion with total length $\underline{x}$ is $\underline{d_x}$ of Equation 6.

In the population of extinct taxa, the expected proportion $\underline{d_e}(x)$ of taxa of the arbitrary length $\underline{x}$ is the normalized product of their frequency in the total sample and their probability of escaping the time-slice of the present. Therefore

$$d_e(x) = \frac{d_x \, p_e(x)}{\int_0^t d_x \, p_e(x) \, dx}.$$

(16)

$$d_e(x) = \frac{a e^{-ax}\left(1 - \frac{x}{t}\right)}{a\int_0^t e^{-ax}\left(1 - \frac{x}{t}\right) dx},$$

(17)

whence

$$d_e(x) = \frac{a^2 t \left(1 - \frac{x}{t}\right) e^{-ax}}{e^{-at} + at - 1}. \tag{18}$$

From equation (5), and noting that there are no extinct taxa longer than $\underline{t}$,

$$l_e(y) = \frac{a^2 t}{e^{-at} + at - 1} \int_y^t \left(1 - \frac{x}{t}\right) e^{-ax} dx. \tag{19}$$

It follows that

$$l_e(y) = \frac{e^{-ay}(at - ay - 1) + e^{-at}}{e^{-at} + at - 1}. \tag{20}$$

As they should, $\underline{l}_e(0) = 1$ and $\underline{l}_e(\underline{t}) = 0$.

This curve is not linear on a semilog plot but convex, although the convexity will in practice be small.

The "life expectancy" in this biased population is the expected value of $\underline{d}_e(\underline{x})$ and so can be obtained from Equation (18):

$$E_e(0) = \int_0^t x \, d_e(x) \, dx. \tag{21}$$

It can also be obtained by applying Equation (12):

$$E_e(0) = \int_0^t l_e(y) \, dy. \tag{22}$$

Fortunately both methods agree, and

$$E_e(0) = \frac{e^{-at}(at + 2) + at - 2}{a(e^{-at} + at - 1)}. \tag{23}$$

Similarly, for the life expectancy at any age $\underline{x}$,

$$E_e(x) = \frac{e^{-ax}(at - ax - 2) + e^{-at}(at - ax + 2)}{ae^{-ax}(at - ax - 1) + ae^{-at}}. \tag{24}$$

TAXONOMIC SURVIVORSHIP CURVES

As must be the case, the life expectancy estimated directly from the distribution of extinct taxa is less than that of the unbiased total sample.

Because t is known and $E_e(0)$ is simply the mean length of all extinct taxa, Equation (23) gives an unbiased estimate of a. Unfortunately an analytic solution seems impossible and a must be obtained by iteration. We then can get unbiased estimates of all other parameters of the total population by using Equations (2) through (14). In practice, t is often not known (or lacks a unique value) because most subtaxa of a group may originate much later than the group itself did. In such cases the origin of the group and the start of its major diversification provide limits on t, and (ceteris paribus) the true value of a will lie between those given by these two estimates.

Living Taxa. The situation here is complicated by the fact that the total duration of some living taxa may be greater than t. In fact all such taxa will be living, because the time-slice of the present is sure to cut them. It is necessary to make separate evaluations of $d_\ell(x)$, the proportion of all living taxa that have total duration x, for two cases: $x \leqslant t$ and $x \geqslant t$.

For $x \leqslant t$, the probability that a taxon will be alive, $P_\ell(x | x \leqslant t)$, is

$$p_\ell(x | x \leqslant t) = \frac{x}{t}. \tag{25}$$

For $x \geqslant t$, $P_\ell(x) = 1$. The rest of the derivation of the equation for $d_\ell(x)$ parallels that for $d_e(x)$, so we have

$$d_\ell(x | x \leqslant t) = \frac{d_x p_\ell(x | x \leqslant t)}{\int_0^t d_x p_\ell(x | x \leqslant t) dx + \int_t^\infty d_x p_\ell(x \geqslant t) dx}. \tag{26}$$

Substituting as in Equation (17) and evaluating,

$$d_\ell(x | x \leqslant t) = \frac{a^2 x e^{-ax}}{1 - e^{-at}}. \tag{27}$$

Similarly, substituting $P_\ell(x | x \geqslant t)$ for $P_\ell(x | x \leqslant t)$ in the numerator of Equation (26),

$$d_\ell(x | x \geqslant t) = \frac{a^2 t e^{-ax}}{1 - e^{-at}}. \tag{28}$$

The proportion $q(x \leqslant t)$ of living taxa whose total length is less than t is

$$q(x \leqslant t) = \int_0^t d_\ell(x | x \leqslant t) dx, \tag{29}$$

or

$$q(x \leq t) = \frac{1 - e^{-at}(at + 1)}{1 - e^{-at}} .$$ (30)

Similarly,

$$q(x \geq t) = \frac{ate^{-at}}{1 - e^{-at}} .$$ (31)

Fortunately $\underline{q}(\underline{x} \leq \underline{t}) + \underline{q}(\underline{x} \geq \underline{t}) = 1.$

It is also necessary to know $\underline{d}'_{\ell}(\underline{x}|\underline{x} \leq \underline{t})$, the proportion of all living taxa with total length less than $\underline{t}$, which have total length $\underline{x}$. Its derivation is that of Equation (26) but the second integral in the denominator is absent.

$$d'_{\ell}(x|x \leq t) = \frac{a^2 x e^{-ax}}{1 - e^{-at}(at + 1)} .$$ (32)

When $\underline{x} \leq \underline{t}$, the random time-slice of the present (or of late-Permian extinctions, etc.) can cut anywhere with equal effect. Therefore the proportion $\underline{r}(\underline{x} \leq \underline{t})$ of $d'_{\ell}(\underline{x}|\underline{x} \leq \underline{t})$ that have a duration before the present of at least $\underline{y}$, is

$$r(x \leq t) = \frac{x - y}{x} ,$$ (33)

where $\underline{y}$ is uniformly distributed in the interval $(0, \underline{x})$.

I define $\underline{l}'_{\underline{y}}(\underline{x}|\underline{x} \leq \underline{t})$ as the proportion of living taxa with total duration less than $\underline{t}$, which have a duration of at least $\underline{y}$ before the present.

$$\ell'_{y}(x|x \leq t) = \int_{y}^{t} r(x \leq t) d'_{\ell}(x|x \leq t) dx .$$ (34)

Substituting and evaluating,

$$\ell'_{y}(x|x \leq t) = \frac{e^{-ay} - e^{-at}(at - ay + 1)}{1 - e^{-at}(at + 1)} .$$ (35)

TAXONOMIC SURVIVORSHIP CURVES

For living taxa with total durations greater than t, l'_y does not depend on the total duration. It depends only on the time of origination, which can be anywhere between 0 and t with equal probability. Therefore

$$\ell'_y\left(x \mid x \geq t\right) = \frac{t-y}{t}. \tag{36}$$

It is now possible to evaluate $l_\ell(x)$, the longevity to the present of taxa now alive.

$$\ell_\ell(x) = \ell'_x\left(y \mid y \leq t\right) q\left(y \leq t\right) + \ell'_x\left(y \mid y \geq t\right) q\left(y \geq t\right). \tag{37}$$

Substituting, this simplifies to

$$\ell_\ell(x) = \frac{e^{-ax} - e^{-at}}{1 - e^{-at}}, \tag{38}$$

which is a mildly convex curve on a semilog plot.

The "life expectancy" of the observed durations of living taxa can be evaluated like that for extinct taxa, whence

$$E_\ell(0) = \frac{1 - e^{-at}(at+1)}{a(1-e^{-at})}, \tag{39}$$

a greater value than that for the total sample. Again, a can be estimated from the mean duration, to the present, of living taxa. The average time back from the present to any age x of taxa now alive is

$$E_\ell(x) = \frac{e^{-ax} - e^{-at}(at - ax + 1)}{a(e^{-ax} - e^{-at})}. \tag{40}$$

The "life expectancy" for taxa now alive, given circumstances like those in the past, is the same as for a taxon at its origin (Equation 13) if the probability of extinction is unrelated to age.

Living and Extinct Taxa. As t increases without limit, the various parameters estimated from the living and extinct subpopulations approach those of the total population.

The proportion of taxa (with a fossil record) that are still living, or that were living at any time in the past, can be calculated for the theoretical case. The closeness to this value of the observed proportion is one measure of (among other things) how average a time the present is with respect to the group considered. (The closeness of the

estimates of $\underline{a}$ from Equations (23) and (39) gives another such measure, and there are many others possible.)

$$P(\text{living}) = P(x \geq t) + P(x \leq t)\left(\frac{E_0(x \leq t)}{t}\right). \quad (41)$$

$$P(\text{living}) = \ell_t + \frac{1}{t}\int_0^t \ell_x \, dx, \quad (42)$$

or

$$P(\text{living}) = \frac{e^{-at}(at-1)+1}{at}, \quad (43)$$

whence

$$P(\text{extinct}) = \frac{(1-e^{-at})(at-1)}{at}. \quad (44)$$

When the number of half-lives since $\underline{t}$ is less than about half of $\log_{10} N_0$ as found empirically, equilibrium methods for estimating $\underline{l}_x$ for living taxa fail. In this case, and the method is unbiased in all cases under the Law of Constant Extinction, the true $\underline{l}_x$ curve for living taxa has to be estimated by converting the numbers of living taxa at each age into the numbers of extinct taxa of each total duration; all taxa will sometime become extinct if the Law of Constant Extinction applies to them.

The conversion of living taxa into extinct ones simply takes the observed number of living taxa of each age and lets them become extinct at the rate estimated from Equations (23) and (39). The taxa are then cumulated as for other extinct taxa, and can be combined directly with them if desired. My plots (Van Valen, 1973a) of living taxa used this method in an earlier and simpler form. The overall shape of these curves is appropriate, but they should be shifted to the right by an amount equal to the life expectancy.

When a stable age distribution is approached closely enough for equilibrium methods to work, as for species and even genera in most cases, and families in many cases, a method given by Kaplan and Meier (1958) seems best. This method estimates $\underline{l}_x$, from which $\underline{a}$ can be determined immediately by Equation (2), or, better, by plotting $\underline{l}_x$ as a survivorship curve to average out sampling error. There is no assumption as to the shape of the survivorship curve, and living and extinct taxa are both used.

The method uses data in the form of a life table, living taxa being directly included with extinct ones. $\underline{n}_x$ is the number of taxa still

TAXONOMIC SURVIVORSHIP CURVES

present at age $\underline{x}$, including those becoming extinct at that age. However, when a living taxon drops out at the same age at which another taxon becomes extinct, the extinction is taken to occur slightly before that age. Then

$$\ell_x = \prod_{y=1}^{x} \left(\frac{m_y - 1}{m_y} \right) \tag{45}$$

Gross and Clark (1975, p. 46) give a fully worked-out numerical example for some simple data.

HETEROGENEITY

It is easy to prove that, when two loglinear survivorship curves are combined, the resulting curve is concave. The steeper curve contributes only to the early part of the combined curve, the later part being nearly that of the gentler curve. This result is quite general and can be formalized, but its applicability to real data is less than universal.

For instance, if the steeper curve has many fewer initial taxa than does the gentler curve, the concavity will be so slight as to be undetectable. The same is true for curves differing little in slope. There are too many ways in which curves can be combined for there to be an easily statable rule on the detectability of heterogeneity. However, I have done a number of simulations and summarize the results to provide the general flavor of the situation.

When the taxon with the gentler slope is the more numerous, even a large difference in slope is poorly detectable unless the numbers of subtaxa differ by a factor of less than about 2. When the taxon with the steeper slope is the more numerous, detectability depends merely on the difference in slope; a difference in slope small enough to be poorly detectable with 50 or 100 subtaxa is uninteresting unless the number of subtaxa are nearly equal. With equal abundance, the combination of two or more curves differing in slope by a factor of less than about 3 is poorly detectable. These results of course depend on sample sizes and extraneous variation; the results given are for no extraneous variation. It is therefore impossible to say with any precision how much variation in susceptibility to extinction may be contained in a roughly loglinear survivorship curve, but biological judgment at least has a framework in which to operate.

A convex curve, for which the probability of extinction per taxon increases with age, could arise from a real increase in the number of interacting taxa over time without a corresponding increase in the energy availability. Each taxon would have a progressively smaller average control of trophic energy and would be buffeted by progressively more competing taxa. The effect would depend on the rate of increase relative to the expected longevity. It requires a shorter expected longevity for geologically later taxa in the interacting group; this would be the crucial test.

DISCUSSION

Because of the lower effect of the specific pecularities of a single stretch of time, the averaging effect of many overlapping intervals predominating, the extinction rate as estimated from extinct taxa will ordinarily be better than the estimate from living taxa. In fact sometimes the latter is wrong

by more than its own value. Living taxa often also include a few with longer observed longevities than would be expected with a single extinction rate. This phenomenon is the basis for the bradytely postulated by Simpson (1944) and usually misinterpreted by others later.

Raup (1975) and others have advocated testing taxonomic survivorship curves for loglinearity. I think such an exercise is futile because the null hypothesis isn't well defined. On the one hand, we know that the observed curves can't be precisely loglinear because of inaccuracies and biases in the data which can be demonstrated independently of the curves (Van Valen, 1973a). This in itself suffices to disprove strict loglinearity; tests on the shape of the curves themselves are superfluous and have much less power. Quantitative adjustment for the biases would produce curves which would be amenable for statistical testing. However, we don't know enough to make such adjustments; therefore there is nothing to test.

A useful approach would be to see what proportion of the total variance of longevities is "explained" by loglinearity. (There is only one real variable, but the geometry in relation to the variance about the expected line is like that in the case of a regression.) This would give a joint estimate of the effects of all biases plus sampling error plus measurement error of both longevity and geologic time. Unfortunately this is a difficult and unsolved problem because of the constraint that the points of a survivorship curve aren't mutually independent. One could fit gamma or Weibull distributions (on which see Gross and Clark, 1975) and see how closely the respective parameters approach those of the declining exponential, but this is hardly more than curvefitting and would give no information on the amount of contribution of nonlinear effects.

I note here an important mistake in Van Valen (1973a). Equation (1), which gives the basic formula for macarthurs, should read

$$ma = \frac{-\log_2 (1-P)}{2t}.$$

(46)

The mistake (but not the correction) was kindly pointed out to me by D.E. Simanek.

Among the causes of irregularities in survivorship curves there are some for deviations of the overall shape of the survivorship curve from loglinearity. They must be evaluated in each case and of course require positive evidence. For instance, the major explanation of the convex survivorship curve for echinoid families, as already mentioned (Van Valen, 1973a, p.9), is that there are few pre-Mesozoic families. The convexity occurs between about 130 and 200 million years and the half-life of echinoid families is more than 50 million years. It is obvious from the original data that the observed convexity results from the fact that there hasn't been enough time yet for loglinearity to be established over the longer intervals. The same phenomenon occurs even more strongly for families of mammals, for which I showed (Van Valen, 1973a, pp.8-9) that removal of the bias produces loglinearity.

It may be, as Raup (1975) believes, that there is a strong disposition by taxonomists to lump smaller supraspecific taxa and split larger ones.

TAXONOMIC SURVIVORSHIP CURVES

If so, a convexity in survivorship curves would result because (1) the bias would concentrate sizes of taxa toward the middle and (2) the probability of extinction is inversely related to the number of subtaxa. Simpson (1961, p.134) finds the bias weak and my experience agrees with his. My evidence (Van Valen, 1973b) on consistency of size of subtaxa among different groups could result, as I noted there, from either taxonomic bias or evolutionary patterns. These possible causes have not yet been tested, but I suspect both contribute. The bias in survivorship curves produced by splitting larger taxa is in fact the only one I have considered (aside from real exceptions) for which I have found no examples.

My paper (Van Valen, 1973a) was submitted in 1972 to Science, which rejected it for a reason relevant here. The one referee who believed he understood the paper thought that, at least initially, the curves should be concave. (Damn the data; full speed ahead.) This expectation is the reverse of that from the preceding argument and results from the belief that taxa living in "archipelagoes, ancient lakes, etc. for which there is little if any fossil record" should be more susceptible than others to extinction, thus biasing the observed curves away from concavity. I showed how this sort of argument, which can be generalized, fails to affect (or account for) the overall linearity; in fact I have more recently found a formally similar situation in the loglinear survivorship of patients with the chronic leukemias. However, it should at least be clear that the detailed shape of taxonomic survivorship curves is a somewhat complex subject.

Raup (1978) has also noted that if species follow the Law of Constant Extinction then higher taxa composed of random assemblages of species will not do so. It follows that in order for higher taxa to show constant extinction their component subtaxa must become extinct nonrandomly. The extinctions of the subtaxa must be positively correlated, as if similar phenomena were affecting them jointly more than they were affecting subtaxa of other higher taxa. Because of this effect, which I mentioned too, I gave evidence (Van Valen, 1973a, pp. 12-14) that such nonrandomness does at least sometimes occur. Thus one must consider biological effects as well as numbers. In fact this was an aspect of my motivation for proposing the Red Queen's Hypothesis. Interactions of taxa are in some rather large part nonrandom (in perhaps any sense of this word) even if certain analyses aren't powerful enough to discover this.

ACKNOWLEDGMENTS

LITERATURE CITED

Foin, T.C., J.W. Valentine, and F.J. Ayala. 1975. Extinction of taxa and Van Valen's law. Nature 257:514-515.

Gross, A. J., and V.A. Clark. 1975. Survival Distributions: Reliability application in the Biomedical Sciences. New York: John Wiley and Sons. 331 pp.

Kaplan, E.L., and P. Meier. 1958. Nonparametric estimation from incomplete
    observations. Journal of the American Statistical Association 53:457-481.
Raup, D.M. 1975. Van Valen's Law. Paleobiology 1:82-96
_____. 1978. Cohort analysis of generic survivorship. Paleobiology 4:1-15.
Salthe, S.N. 1975. Some comments on Van Valen's law of extinction.
    Paleobiology 1:356-358.
Sepkoski, J.J., Jr. 1975. Stratigraphic biases in the analysis of taxonomic
    survivorship. Paleobiology 1:343-355.
Simpson, G.G. 1944. Tempo and Mode in Evolution. New York: Columbia Univ.
    Press. 237 pp.
_____. 1961. Principles of Animal Taxonomy. New York: Columbia Univ.
    Press. 247 pp.
Van Valen, L. 1973a. A new evolutionary law. Evol. Theory 1:1-30.
_____. 1973b. Are categories in different phyla comparable? Taxon 22:333-373
_____. 1975 [Reply to Foin, Valentine, and Ayala, 1975.] Nature 257:515-516.
_____. 1976a. The Red Queen lives. Nature 260:575.
_____. 1976b. Energy and evolution. Evolutionary Theory 1:179-229.