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ESTIMATING TAXONOMIC DIVERSITY, EXTINCTION RATES AND SPECIATION RATES FROM
FOSSIL DATA USING CAPTURE-RECAPTURE MODELS

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ABSTRACT.--- Methods currently used to estimate taxonomic extinction probabilities from fossil data generally assume that the probability of encountering a specimen in a particular stratum, given that the taxon was extant in the time period and location represented by the stratum, either equals one or else is a constant for all strata. Methods used to estimate taxonomic diversity (number of taxa) and speciation rate generally assume that encounter probabilities equal one. We suspect that these assumptions are often false. Capture-recapture models were historically developed for estimation in the face of variable and unknown sampling probabilities. These models can thus be used to estimate parameters of interest from paleobiological data when encounter probabilities are unknown and variable over time. These models also permit estimation of sampling variances, and goodness-of-fit tests are available for assessing the fit of data to most models. Here, we describe capture-recapture models that should be useful in paleobiological analyses and discuss underlying assumptions. We illustrate these models with examples and discuss aspects of study design. We conclude that these models should prove useful in paleobiological analyses.

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Introduction

A number of interesting hypotheses in paleobiology require information on taxonomic extinction rates, rates of speciation and species diversity or richness (Van Valen 1973, Stanley 1979, Rosenzweig and Taylor 1980). Several workers have recognized the similarity between phylogenetic dynamics within major taxonomic groups and the dynamics of individual populations, and have applied some of the methodologies of population dynamics and demography to paleobiological problems (e.g., Simpson 1953; Kurten 1954; Van Valen 1973; Raup 1975, 1978; Stanley 1979). Most of these borrowed methodologies were initially developed by human demographers whose data base consisted of relatively accurate time-specific and age-specific tabulations of births and deaths. The data base of the paleobiologist consists of tabulations of taxa known, through fossilized remains or impressions, to have been present during various periods of geologic time. In terms of estimating parameters of interest, the important difference between the data bases of the demographer and the paleobiologist is the "completeness" of the sampling effort. Many of the methodologies of demography (e.g., see Keyfitz 1968) effectively ignore sampling problems and assume that reasonably complete records of births, deaths and total population size exist. However, paleobiologists are not able to obtain complete records (i.e., the probability of a taxon appearing in a sample from a particular time period is often considerably less than 1), and their estimation problems thus correspond much more closely to those of the animal population ecologist than to those of the human demographer. The inability to obtain complete samples led animal population ecologists to develop intuitive capture-recapture estimators (Petersen 1896, Lincoln 1930)

and, eventually, probabilistic capture-recapture models (e.g., see Cormack 1968, 1979; Pollock 1981). We believe that capture-recapture models provide the appropriate conceptual framework and methodology for estimating many parameters of interest to the paleobiologist. The applicability of a particular class of capture-recapture models to the estimation of fossil species diversity has already been recognized (Rosenzweig and Duek 1979, Rosenzweig and Taylor 1980).

In this paper, we introduce a variety of available capture-recapture models and discuss their applicability to the estimation of extinction rates, speciation rates and species numbers from fossil data. We do not provide a detailed or extensive review of capture-recapture models. Instead we have selected for discussion the models that we suspect will be most useful to paleobiologists. General reviews of capture-recapture models have been provided by Cormack (1968, 1979), Seber (1973), and Begon (1979). Pollock (1981) and Nichols et al. (1981) presented recent reviews and Brownie et al. (1978) and Otis et al. (1978) review specific classes of models. We have also attempted to provide a nonmathematical discussion of the underlying statistical models and their associated estimators, although readers interested in statistical detail will be directed to the appropriate source references.

Capture-Recapture Models

Background

When applied to animal populations, capture-recapture experiments can typically be thought of in the following way. The population under study is sampled K times where K is usually more than two. Each sampling time, every unmarked animal caught is uniquely marked; previously marked animals have their captures recorded; and then all of the animals are released back into

the population. At the end of the experiment the biologist has the complete capture history of every animal handled.

Capture-recapture models are often classified according to their assumptions about population closure. Closed population models are used with populations that do not lose or gain animals through death, birth, or migration during the sampling period. Open population models are used with populations that do change over the period of investigation through deaths and emigration, births and immigration, or both sets of factors. Closed population models are therefore more likely to be used in short-term studies and open population models in long term studies. We also describe a "robust procedure" which combines both closed and open models in the same study (Pollock 1982).

Closed Population Models

Closed population models may be useful in estimating species diversity (i.e., the total number of species present, either within a taxon of interest or across taxa) within geologic strata (Rosenzweig and Duek 1979, Rosenzweig and Taylor 1980). Because of the assumption of population closure, these models could not be applied to samples from 2 different strata unless it could be assumed that the probability of an extinction or speciation event occurring during the time interval represented by the distance between strata was negligible. We suspect that this assumption will seldom be a reasonable one. We can envision 3 general kinds of fossil sampling schemes within a stratum of interest and the distinction between them is very important to the use and choice of closed population models.

No Sampling Units, Taxonomic Presence-Absence Data. In the first scheme, the paleobiologist simply records presence or absence of each

taxon regardless of the number of individuals of that taxon actually encountered and regardless of the area or subareas searched. While such presence-absence data can be used with open models across strata, they cannot be used with closed models within strata to estimate number of taxa.

Sampling Units, Taxonomic Presence-Absence Data. In the second kind of sampling scheme, the paleobiologist records presence or absence of each taxon of interest in each of a number of sampling units within a stratum. For example, the sampling units might be areas or volumes of sediment within the stratum that are searched for fossils. These sampling units are analogous to the different trapping periods (e.g., each of the days on which animals are captured) of the animal capture-recapture application. Four closed population models seem potentially relevant to paleobiological estimation under this kind of sampling scheme, and they differ in their assumptions about sources of variation in "encounter probability" (analogous to capture probability). We define encounter probability as the probability of encountering a fossil representative of a specific taxon in a particular sampling unit, given that members of that taxon were extant during the time period represented by the stratum, and inhabited the geographical area represented by the samples.

The most simple model, M_0 , assumes that encounter probability varies neither among taxa nor among sampling units (Otis et al. 1978:21-24). Every taxon has the same probability of being encountered in every sampling unit. This assumption yields a multinomial model with only 2 parameters: total number of taxa, N , and encounter probability, p . When there are more than 2 sampling units, the maximum likelihood (ML) estimator of N does not exist in closed form and must be computed numerically. An estimator for the variance of N is also available (Otis et al. 1978). The estimator N

is not robust to variation in encounter probability and is negatively biased when encounter probability varies from 1 taxon to another (heterogeneity of encounter probability).

A similar but somewhat less restrictive model, M_t , permits encounter probability to vary among sampling units but assumes that within each unit all taxa have equal encounter probabilities (Darroch 1958, Otis et al. 1978:24-28). This model is characterized by $K+1$ parameters (where K denotes the number of sampling units): total number of taxa, N , and the K encounter probabilities, p_j where $j=1, \dots, K$. The ML estimator, \hat{N} , must again generally be computed numerically. This estimator, \hat{N} , also exhibits a substantial negative bias when heterogeneity of encounter probability occurs (see Otis et al. 1978).

The assumption of equal encounter probabilities among taxa in models M_0 and M_t will probably greatly restrict their applicability in paleobiological work. This assumption is relaxed in model M_h (Burnham and Overton 1978, 1979; Otis et al. 1978:33-37), which assumes that each different taxon has a specific encounter probability which is constant for all sampling units. Conceptually, we can think of these taxon - specific encounter probabilities, p_i (where i indexes taxa), as a random sample of size N from some probability distribution $F(p)$. There is no entirely satisfactory way to derive an estimator of N from this model. Burnham used the "jackknife" method of bias reduction and obtained a series of estimators of the following form:

$$\hat{N}_\ell = \sum_{i=1}^K c_{i\ell} f_i \quad (1)$$

where \hat{N}_ℓ is the diversity estimator corresponding to order ℓ of the jackknife procedure, f_i is the number of taxa from which exactly i individuals are encountered, $c_{i\ell}$ are constants generated by the jackknife

procedure of order l , and K is the number of sampling units (Otis et al. 1978). Otis et al. (1978:35) concluded that this was the most robust estimator of those they considered (also see Burnham and Overton 1979).

In model M_{th} , variation in encounter probability is associated both with individual taxa and with different sampling units (Otis et al. 1978:38-40). No estimators are currently available for this model.

The investigator must decide which, if any, of the 4 described models is appropriate for his data set. Otis et al. (1978) describe goodness-of-fit tests of specific models to the data and likelihood ratio tests between specific models and more general alternatives. They also describe a model selection procedure using a discriminant function built with simulated data. Computation of estimators, model test statistics and model selection values are all carried out by a computer program, CAPTURE, developed by Otis et al. (1978; also see White et al. 1978, White et al. 1982). It should be noted that Otis et al. (1978) actually consider 8 capture-recapture models, but 4 of these incorporate a behavioral response to trapping, a situation for which there is no reasonable analog in paleobiological studies.

It should be clear that the magnitude of the encounter probability and the sources of variation in this parameter are extremely important in the discussed models. Precision of the resulting diversity estimate is directly related to this probability, which is expected to increase with the size of the sampling units. However, the number of sampling units is also important, and at least 5 and preferably 10 should be used. The sampling scheme chosen in any particular study will thus represent a compromise between practical limitations (e.g., available time and effort), and the desirability of a number of relatively large sampling units (e.g., insuring encounter probabilities of at least 0.1). Detailed discussions of study design in the

animal capture-recapture situation are provided by Otis et al. (1978:74-81) and Pollock (1981).

In cases where both taxonomic heterogeneity and variation among sampling units exist (model M_{th}), no estimator for diversity is available. It is thus desirable to reduce or eliminate at least one of these sources of variation in encounter probability. Variation among sampling units can be reduced by using units of equal size (e.g., surface area or volume) and by expending equal searching effort in all units. Heterogeneity of encounter probability can probably be reduced by estimating diversity within specific taxonomic groupings and then summing these to obtain an overall community estimate (if the latter is desired). This approach may often be preferable to combining data from taxa covering a broad range of taxonomic groups which might be expected a priori to exhibit substantial variation in encounter probability. Both taxonomic heterogeneity and variation between sampling units can occur despite these efforts to eliminate them. For example, even if the investigator expends equal effort on all sampling units, it may be that taxa are distributed very unevenly over units as a result of microhabitat preferences, gregarious behavior patterns or any other factor tending to produce clumped distributions of taxa. Heterogeneity of encounter probability can result from differences in population density among taxa at the time period and location of interest and from intertaxa differences in the probability of being preserved or fossilized. We suspect that taxonomic heterogeneity will be the most common source of variation in encounter probability and that M_h will thus prove to be the most useful model for paleobiologists.

No Sampling Units, Taxonomic Frequency Data. In the third general sampling scheme, the paleobiologist does not divide the searched area

into sampling units but simply records the number of individuals in each taxon found during all sampling within the stratum. The data produced by this kind of sampling effort form a frequency distribution of number of individuals encountered per taxon. This is analogous to the frequency distribution of captures per individual in the animal population estimation context. Burnham and Overton (1979) pointed out that their model, M_h , can be made to fit this form of sampling by taking the limiting values of the coefficients c_{ij} as K becomes infinite (see equation 1). This model and its relevant characteristics have already been discussed.

Open Population Models

Open population models can be used not only to estimate species diversity at specific time periods (strata), but also extinction probabilities and numbers of new species or taxa occurring between periods.

Jolly-Seber Model. The open model which is probably of greatest potential interest to paleobiologists is the Jolly-Seber model (Jolly 1965, Seber 1965, Seber 1973: 196-232). This model can be used, for example, when the paleobiologist records the taxa present in each of a series of strata representing different time periods at a particular sampling site. The following basic assumptions are required by the model:

- (1) Every taxon in the group of interest has the same encounter probability, p_i , within each stratum, i ($i=1, \dots, K$; where stratum 1 corresponds to the oldest time period and stratum K the most recent), given that it was extant in the sampled location at the time period corresponding to the stratum.
- (2) Every taxon in the group of interest has the same probability (ϕ_i) of surviving the period separating strata i and $i+1$, given that it is

extant in the sampled location during the period represented by stratum i ($i=1, \dots, K-1$).

- (3) The differences between time periods represented by samples taken within the same stratum are short relative to the time separating adjacent strata, i and $i+1$.
- (4) If all representatives of a taxon leave the general location represented by the sample or become locally extinct there, they do not become reestablished there in time periods represented by subsequent samples.

Consequences of deviations from these assumptions will be discussed later.

The Jolly-Seber model can be expressed as the product of multinomial or hypergeometric distributions (see discussion of these 2 approaches in Cormack 1979). One means of illustrating the logic underlying the model is to write out expected values of some of the statistics obtained via the sampling process. For example, let a_{ij} denote the number of taxa encountered in stratum j that were last encountered in stratum i , and let n_i denote the total number of taxa encountered in stratum i . We can then write the expectations of all a_{ij} in a sampling experiment in terms of n_i , ϕ_i , and p_i , and we have done so for a small experiment in Table 1.

The quantities of principal interest in the Jolly-Seber model are ϕ_i , N_i (total extant taxa in the group of interest at the time represented by stratum i), and B_i (number of new taxa originating within the group of interest between periods i and $i+1$ and extant at the time represented by stratum $i+1$). Here we will point out the intuitive nature of the estimators for these quantities (also see Jolly 1965; Cormack 1972, 1973). Define M_i as the total number of taxa extant at time i that were encountered in sampling efforts at strata representing earlier time periods, and m_i as the number of these M_i taxa that are encountered again in stratum i . If the 4 listed assumptions are

true, then:

$$m_i/n_i \simeq M_i/N_i$$

and this expression yields the following estimator for N_i :

$$\hat{N}_i = n_i M_i / m_i \quad . \quad (2)$$

The n_i and m_i are observable random variables obtained directly from the sampling effort. However, M_i is a random variable which is not known but must be estimated.

In order to estimate M_i , we must first note that there are 2 groups of taxa extant at i that have been encountered at some stratum $\leq i$. One group is simply comprised of the taxa encountered at i , n_i , and we define r_i as the number of these taxa that are encountered in some more recent stratum ($>i$). The other group is made up of taxa extant at i , and encountered in some older stratum ($<i$), but not in i ($(M_i - m_i)$ taxa are in this group). Define z_i as the number of taxa encountered both in an older stratum and in a more recent stratum than i , but not in i itself. If our assumptions are true, then the proportion of taxa from each of these groups which is seen again (at some stratum $>i$) should be equal, or:

$$z_i / (M_i - m_i) \simeq r_i / n_i$$

We can then solve for M_i and obtain our estimator as:

$$\hat{M}_i = n_i z_i / r_i + m_i \quad . \quad (3)$$

This estimator for M_i given in (3) allows us not only to estimate N_i using (2) but also to estimate ϕ_i as:

$$\hat{\phi}_i = \hat{M}_{i+1} / (\hat{M}_i - m_i + n_i) \quad (4)$$

This estimator is also intuitively appealing. \hat{M}_{i+1} is simply the number of taxa extant at $i+1$ and also known to have been extant at some previous period ($\leq i$). The expression $\hat{M}_i - m_i + n_i$ then represents the number of taxa extant at i and known to have been extant at some period $\leq i$.

Finally, an intuitive estimator for B_i is given by:

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i \hat{N}_i \quad (5)$$

or the total estimated number of taxa extant at $i+1$ minus the estimated number of these taxa that were survivors from time i . Additional discussions of these estimators (2)-(5) and their approximate large-sample variances is presented by Seber (1973:205).

Effects of deviations in Jolly-Seber model assumptions have been fairly well-studied. The assumption of constant p_i for all taxa within the group of interest may often be false for the same reasons discussed under closed population models. Again, restriction of the group of interest to closely-related taxa will help reduce taxonomic heterogeneity of p_i . However, such factors as differing population densities of the taxa of interest and differences in tendency to be fossilized can still result in heterogeneity. Heterogeneity of encounter probabilities has been studied by Carothers (1973) and Gilbert (1973) and has been shown to produce substantial negative biases in estimates of N_i . Such heterogeneity also produces biases in estimates of ψ_i , although these biases are considerably smaller than those for \hat{N}_i (Carothers 1973, Gilbert 1973).

Heterogeneity of ϕ_i among taxa may certainly occur, but we have little intuition about the degree of heterogeneity to expect. Taxonomic survival probabilities (and hence extinction probabilities, $1-\phi_i$) will be a function of number of subtaxa and absolute sizes of member populations. For example, genera represented by large numbers of species should exhibit higher survival probabilities than those represented by a single species, if other factors are equal. Similarly, a species represented by a very large population (i.e., containing many individuals) should exhibit a higher survival probability than one represented by a small population. Ecological differences between

taxa in such factors as competitor populations, predator populations and life history patterns could also result in taxonomic heterogeneity of ψ_i . The effect of heterogeneous ϕ_i on Jolly-Seber estimates has been recently studied by Pollock, Nichols and Hines (in prep.). In the case of heterogeneous survival rates and equal encounter probabilities, the $\hat{\phi}_i$ overestimate average survival probability and the \hat{N}_i are negatively biased. When both survival and encounter probabilities vary across taxa, then the direction of bias in Jolly-Seber estimates depends on the relationship between survival and encounter probability of a taxon. If a negative relationship exists (i.e., if taxa with high survival probabilities tend to have low encounter probabilities and vice versa) then $\hat{\psi}_i$ will generally be negatively biased and \hat{N}_i positively biased. If a positive relationship holds (i.e., if taxa with high survival probabilities tend to have high encounter probabilities and vice versa) then $\hat{\phi}_i$ will be positively biased and \hat{N}_i negatively biased. If taxonomic heterogeneity exists in both survival and encounter probability, then we suspect that they will often exhibit a positive relationship, because such factors as number of subtaxa and population densities of subtaxa should influence survival and encounter probabilities in the same direction.

It is difficult to predict how frequently and seriously the assumption of no temporary emigration or temporary local extinction will be violated. As an example, if a particular sampling location is believed to have passed from a terrestrial to an aquatic and back to a terrestrial environment again, over geologic time, then this assumption could certainly be invalid for many taxa. Other less drastic changes in local ecological conditions through geologic time could also result in temporary absences of taxa in times represented by some samples. This temporary emigration problem can be reduced

by restricting analyses to sequences of adjacent strata believed to represent generally similar ecological environments. If sudden changes are perceived in a series of strata, then the series can be broken into separate component series for analysis. The effect of temporary emigration is to produce positive bias in both \hat{N}_i and $\hat{\phi}_i$ (Balser 1981).

The assumption of short intrasample period relative to intersample period can be met through reasonable choice of sample strata. If this assumption is not met, then the whole idea of estimating a time-specific diversity or a probability of surviving from a time represented by sample i to one represented by sample $i+1$ loses meaning. Violation of this assumption can result in heterogeneity of survival probabilities if taxa encountered in different portions of a strata have substantially different time periods to survive in order to appear in sample $i+1$.

Several methods are available for assessing the reasonableness of the Jolly-Seber model for actual data sets. Specific tests are available for heterogeneity of encounter probability (Leslie 1958, Carothers 1971) and temporary emigration (Balser 1981). General goodness-of-fit tests have been described by Seber (1973:223-224), Leslie et al. (1953) and Jolly (1982) and we have found the latter 2 to be most useful with capture-recapture data sets (see Nichols et al. 1981).

Modifications (both generalizations and restrictions) of the Jolly-Seber model have been developed for capture-recapture experiments and some of these may be useful to paleobiologists. Jolly (1979, 1982) and Crosbie (1979) have developed restrictive models with survival and/or capture probabilities constant over all sampling periods. Model parameters can be estimated with greater precision in the cases where these models do apply. The restriction that encounter probabilities are equal for all strata is

reasonable in the paleobiological context, although it may seldom be true. The restriction of equal survival probabilities is reasonable in the paleobiological context if the time periods believed to separate adjacent strata, i and $i+1$, are equal for all i . If intersample time periods are not equal, then the hypothesis of equal ϕ_i makes little sense. However, the hypothesis of equal probabilities of surviving equivalent periods of time is still logical, and Crosbie (1979) has developed a model for use in this situation. Crosbie (1979) has also developed a modified Jolly-Seber model with different definitions for birth numbers and population size. In this modified Jolly-Seber model, an estimate is obtained of the total number of individuals (or taxa) present at any time over the entire period of sampling, even if the lifespan of some individuals (or taxa) did not happen to span a sampling period (or sampled stratum). Similarly estimates of birth numbers include individuals that do not survive until a sampling period. In any case these definitions may be of interest in studies of taxonomic diversity and speciation.

Finally, we note that computer programs have been developed for computing Jolly-Seber estimates from capture-recapture data, and these should also be useful for paleobiological data. Simple programs have been written by Davies (1971) and White (1971), while a more powerful package has been developed by Arnason and Baniuk (1980).

Robust Procedure. Pollock (1982) has recently suggested a sampling design for open population experiments that actually makes use of both open and closed population models. The design was suggested as a means of providing robust estimation even in the presence of heterogeneity of encounter probabilities. In the paleobiological context, we envision this procedure as being useful for the same general situation as described for the Jolly-

Seber model, in which samples are taken from a series of strata representing different time periods at a particular sampling site. Taxonomic presence-absence data for each stratum are sufficient for the Jolly-Seber model, but the robust design additionally requires either the use of separate sampling units or the recording of taxonomic frequency data, within each stratum. These frequency data or data from the different sampling units are then used in conjunction with the closed population models described earlier (specifically M_h) for robust estimation of N_i for each stratum. Data within each stratum are pooled to provide the taxonomic presence-absence data required by the Jolly-Seber model. Survival estimates, which are less affected by heterogeneity of encounter probabilities, are then obtained using the Jolly-Seber model. Finally, the B_i are estimated using equation (5), with the N_i coming from model M_h and the ϕ_i coming from the Jolly-Seber model. Assumptions underlying M_h and the Jolly-Seber model, as well as consequences of their violation, have already been discussed. Pollock (1982) should be consulted for a detailed description of this procedure in the capture-recapture context.

Band Recovery Models

Band recovery models are closely related to the open capture-recapture models and we believe they may be useful for a particular type of paleobiological data. The models were developed to analyze data from experiments in which animals are tagged and released, and their tags returned when they are taken by hunters, trappers or fishermen. Therefore, unlike the general capture-recapture situation, each animal released at period i can only appear as a "recapture" in one subsequent sampling period, $j > i$. The single-age model of Seber (1970) and Robson and Youngs (1971) and similar

reduced-parameter models (Brownie et al. 1978) will probably be useful to paleobiologists.

We believe that band recovery models may be useful with compiled data on the geologic periods of first and last encounters with fossils of specific taxa (e.g., Moore and Teichert 1953-1978, Romer 1966, Sepkoski 1982). Stratigraphic range data of this sort have been the focus of several previous analyses directed at questions about extinction rates (Van Valen 1973; Raup 1975, 1978; Stanley 1979). Jolly-Seber assumptions (1)-(3) are required by the band recovery models (see Pollock and Raveling 1982), except in assumption (1) we deal with a final encounter probability, f_i , instead of p_i . The interpretation of this final encounter probability depends on the form of the data and on the parameterization of the band recovery model. For example, if the Brownie et al. (1978) models are used in conjunction with the data of Raup (1978: Table 1), then f_{i+1} represents the joint probability of surviving from i to $i+1$ (ϕ_i), of being encountered in $i+1$ (p_{i+1}), and of never being encountered again (this latter probability is a function of all survival and encounter probabilities after $i+1$). When using such stratigraphic range data, ϕ_i will generally be interpreted as the probability of surviving from the approximate mid-point of period i to the mid-point of period $i+1$. Assumption (4) for the Jolly-Seber model (the assumption concerning local extinction and subsequent reestablishment) is important for analysis of paleobiological data from a specific sampling location, but should not be relevant to the type of worldwide first and last encounter data that we suggest be used with band recovery models.

The band recovery models of Brownie et al. (1978) are expressed as products of multinomial distributions. Let Q_i denote the number of taxa

encountered in geologic time period i , and let R_{ij} denote the number of taxa first encountered in period i and last encountered in period j . The structure of Model 1 (Brownie et al. 1978:15-20) is illustrated in Table 2, where we write out the expected values of the R_{ij} in terms of the Q_i , ϕ_i and f_i . When considering the logic of Table 2, it is important to recall that f_{i+1} includes the probability of a taxon surviving from period i to $i+1$.

Band recovery models can be used to estimate ϕ_i but not N_i or B_i .

The ML estimator of ϕ_i is:

$$\hat{\phi}_i = \frac{R_i}{Q_i} \frac{(T_i - C_{i+1})}{T_i} \frac{Q_{i+1}}{R_{i+1}} \quad (6)$$

where R_i denotes the number of taxa encountered at i and at some later period, C_i denotes the number of taxa encountered at some period $< i$ and encountered for the last time at i , and T_i is the number of taxa encountered at or before i and encountered for the last time at some period $> i$. An ML estimate of var ϕ_i is also available (Brownie et al. 1978:17).

If the final encounter probability, f_i , differs among the taxa under consideration, but survival probability, ϕ_i , does not, then (6) still provides an unbiased estimate of ϕ_i (Pollock and Raveling 1982). If ϕ_i are heterogeneous among taxa and f_i are either homogeneous, or heterogeneous among taxa but independent of ϕ_i , then $\hat{\phi}_i$ will be positively biased (Pollock and Raveling 1982). If ϕ_i and f_i are heterogeneous among taxa and negatively related within taxa, then $\hat{\phi}_i$ will be negatively biased (Pollock and Raveling 1982). However, if ϕ_i and f_i are heterogeneous and positively related, then $\hat{\phi}_i$ will be positively biased (Nichols et al. 1982). Because of the fact that survival probability is incorporated in f_i , and p_i (also incorporated in f_i) tends to be positively related to survival

probability (see discussion under Jolly-Seber model assumptions), we suspect that positively related f_i and ϕ_i will be common in paleobiological data when heterogeneity does exist. Thus, heterogeneity may often result in overestimation of ϕ_i .

The assumption of short intrasample period relative to intersample period is of particular concern with stratigraphic range compilations. In such compilations first and last encounters are generally assigned to geologic periods or series that may be quite long in duration. Certainly, fossil dating procedures are inexact. If it is generally more likely for a fossil to have come from the middle of a period to which it has been assigned than from the beginning or end of the period, then the short intrasample period assumption may be reasonable. However, if a fossil assigned to a particular period has an equal probability of being from any portion of the period, then the assumption will not be reasonably met. Although we recommend that paleobiologists attempt to use band recovery models for analyzing this general type of data, we have reservations that stem largely from concerns about this assumption.

Goodness-of-fit tests (Brownie et al. 1978) can be used to assess the reasonableness of band recovery model assumptions for specific data sets, but these tests have fairly low power to detect heterogeneity of ϕ_i and f_i for magnitudes of parameter values generally encountered in the bird-banding situation (Nichols et al. 1982). However, we have already found a number of cases using stratigraphic range data from Raup (1978) and Sepkoski (1982) in which goodness-of-fit tests indicate model rejection, so these tests are sufficiently powerful to detect some of the kinds of problems that exist with paleobiological data. A specific test for temporary emigration has been developed by Balser (1981), but we do not believe

that this assumption will be as frequently violated as some others with stratigraphic range data.

Restrictive models assuming constant survival probabilities and both constant survival and final encounter probabilities have been developed for the bird-banding situation (Brownie et al. 1978). We suspect that these models will be of little use in analyzing stratigraphic range data because the time intervals separating sample periods are not equal, and the constant ϕ_i assumption is thus not reasonable. Conroy and Nichols (in prep.) have recently developed a band recovery model assuming constant survival per unit time and have used it to test hypotheses about the constancy of taxonomic extinction rates.

Computer programs for computing parameter estimates and goodness-of-fit test statistics are described in Brownie et al. (1978). Program ESTIMATE includes Model 1 and should be useful for paleobiological analyses.

Examples

Closed Model M_h , Jolly-Seber Model and Robust Design

Sorgenfrei (1958) presented detailed data on Molluscan species in well samples representing the marine Middle Miocene of South Jutland. These data include not only information on the occurrence of species in different well strata, but also on the number of specimens found for each species. The species occurrence data are sufficient for the Jolly-Seber model. However, the specimen frequency data also permit estimation of total species numbers using closed model M_h , and we can thus use the robust design of Pollock (1982).

We restricted our analysis to representatives of Gastropoda found in the "Toftlund, Arnum formation" samples (Sorgenfrei 1958:448-459; Table 15, part 2). In Table 3, we present the summary statistics required by the

Jolly-Seber and M_h models. Use of the n_i , m_i , r_i , and z_i with the Jolly-Seber model permits estimation of number of species, N_i , species survival rate, ϕ_i , and number of new species, B_i . The goodness-of-fit test statistic of Jolly (1982) was computed for these data and it suggested an adequate fit of the model ($\chi^2 = 1.1$, 1df, $P = 0.30$). However, because of our suspicion that fossil encounter probabilities are generally heterogeneous among species, we also estimated N_i using model M_h with the specimen frequency data, f_{ji} and N_i (Burnham and Overton 1979:934-935). The resulting \hat{N}_i were larger in every case than the corresponding Jolly-Seber estimates, which is exactly what is expected when encounter probabilities are heterogeneous. Therefore, we followed Pollock (1982) and used the \hat{N}_i from model M_h , the $\hat{\phi}_i$ from the Jolly-Seber model, and estimated \hat{B}_i using these estimates from both models. The resulting estimates and their estimated standard errors are presented in Table 4.

The estimates of numbers of species were somewhat higher for the 3 more recent samples (Table 4). Number of new species differed significantly from 0.0 only for the 110-115 m sample. Species survival rates were very similar in the 3 samples for which they could be estimated.

Jolly-Seber Model

Schankler (1980) presented detailed data on the occurrence of mammalian species in a series of stratigraphic samples from the Late Eocene record of the Big Horn Basin, Wyoming. We tabulated data from the first (most recent) 19 samples in Fig. 3 of Schankler (1980:104-105) for all 131 listed taxa. Occurrences listed by Schankler (1980:104-105) as taxonomic and stratigraphic uncertainties were not used in the analysis.

When the Jolly-Seber model was used with this data set, the goodness-of-fit test indicated strong rejection of the model ($\chi^2 = 28.0$, 9df,

$P = 0.001$). We selected a subset of these data (samples 8-19) which had good numbers of encounters and computed Jolly-Seber estimates. The goodness-of-fit test statistic indicated better fit to the model ($\chi^2 = 12.7$, 5df, $P = 0.03$) than for the full data set and the estimates appeared to be reasonable. Summary statistics for this data set are presented in Table 5, and Jolly-Seber estimates are shown in Table 6.

Estimates of total taxa ranged from approximately 33 to 56 and survival estimates from 0.81 - 1.00 (Table 6). Estimated numbers of new species are low, but differ significantly from 0.0 for samples 18, 16 and 12. The estimates of encounter probability vary substantially (0.14 - 0.83) and serve to emphasize that estimation methodologies which assume either that all $p_i = 1.00$ or that p_i is constant over all strata ($p_i = p$) are likely to perform poorly with data of this type.

Band Recovery Model 1

Raup (1978) compiled stratigraphic range data from over 17,000 genera and subgenera of Phanerozoic invertebrates. The data were obtained from Moore and Teichert (1953-1978), and consist of the time of first and last encounter of each taxon organized by the 10 major periods of the Phanerozoic. We do not consider this data set to be ideal for our purposes, because we would a priori expect a great deal of heterogeneity in both survival and final encounter probabilities among such a diverse group of organisms. However, this data set was chosen because it is compiled in exactly the form needed for our analysis (Table 1 of Raup 1978) and because it has been used to obtain estimates of extinction probability with other methodologies.

Data on the diagonal of the "time of extinction" matrix of Raup's (1978) Table 1 were not used in our analysis (see the model depicted in Table 2). The remainder of the data were analyzed using Model 1 (Brownie et al. 1978),

and the resulting goodness-of-fit test statistic indicated resounding rejection of the model ($\chi^2 = 655.24$, 31 df, $P \approx 0.00$). However, 2 cells accounted for approximately half of the total χ^2 value, and portions of the data set seemed to fit reasonably well. We, therefore, selected a subset consisting of taxa first seen in the Permian, Triassic, Jurassic, and Cretaceous, and last encountered in the Triassic through the Tertiary (Table 7).

This data set fit Model 1 well ($\chi^2 = 0.88$, 2 df, $p \approx 0.65$) and yielded the estimates in Table 8. The estimated probability of surviving the Permian - Triassic interval was substantially lower than the other 2 survival probability estimates. The survival estimates thus fit well with the suggestion of Raup (1978) and Raup and Sepkoski (1982) that mass extinctions occurred during the Permo-Triassic interval. Thus, despite potential problems with heterogeneity of survival and encounter probabilities, the band recovery model appeared to perform well with the invertebrate fossil data.

Discussion

As with all statistical models of biological phenomena, capture-recapture models are based on assumptions which are seldom, if ever, precisely met. One can only hope that a particular data set has resulted from a process that approximates the selected model sufficiently well to yield accurate estimates. Some of the paleobiological data sets presented in the examples did not fit the capture-recapture models as well as might have been hoped, although even in these cases the models did produce estimates which appeared reasonable. Problems of heterogeneous survival and encounter probabilities and long intrasample time periods may limit the usefulness of the models we have described in some situations.

Much additional work with actual data sets must precede any informed judgment regarding capture-recapture model utility in paleobiology.

Despite some reservations about the ultimate usefulness of these models, however, we believe strongly that they will generally be superior to estimation methods currently in use. This belief results from the fact that methods other than capture-recapture models assume that all extant taxa (or in some cases a constant proportion of extant taxa) are encountered during each sampled period. This assumption is generally believed to be false (e.g., Sepkoski 1975). Some methods make additional restrictive assumptions that can be relaxed and tested using capture-recapture models. Here, we will briefly discuss 2 general approaches that have been used to analyze paleobiological data and present our reasons for believing capture-recapture models to be superior.

The first general approach has been used to estimate diversity and is analogous to that used to estimate population size in many contemporary small mammal capture-recapture studies. Taxonomic diversity (numbers of extant species) for a specific stratum is "estimated" as the number of taxa encountered in that stratum plus the number that were not encountered in the stratum but were encountered in earlier and later strata (and hence known to have been extant at the time representing the stratum of interest). The bias of this estimator, which is always negative, is a function of time-specific extinction and encounter probabilities and can be quite large (Nichols and Pollock in press).

The second general approach, sometimes termed the survivorship approach, is used to estimate extinction probabilities and to draw inferences about temporal variation in these probabilities. In this approach, data are graphically depicted by plotting total number of subtaxa (generally on a

logarithmic scale) on the ordinate versus time on the abscissa. In some cases, the initial number of subtaxa (N_0 , or subtaxa at time $t=0$) is equated with the number of subtaxa first encountered in a specific geologic period (see Raup 1978). Subsequent numbers of period-specific subtaxa (N_t) then represent the number of subtaxa from this initial group that are encountered again in some period $\geq t$. An alternative to this "cohort analysis" approach is to define N_0 as the total number of subtaxa encountered at any time (i.e., the time of first encounter is not relevant here) within the group of interest (e.g., see Van Valen 1973, Raup 1975). Subsequent numbers, N_t , are then defined to be the number of subtaxa whose first and last encounters are separated by $\geq t$ time units.

The survivorship curves produced by the method described above have been subjected to a number of different analyses and interpretations, virtually all of which are based (implicitly or explicitly) on a constant extinction probability model. The model simply expresses N_t as a function of N_0 and the instantaneous extinction probability, λ .

$$N_t = N_0 e^{-\lambda t}$$

or
$$\ln N_t = \ln N_0 - \lambda t \quad (7)$$

If extinction probability is constant over time (and hence if (7) is true), then the $\ln N_t$ vs. t survivorship plot should be linear. In fact, visual assessments of the linearity of such plots have been the basis for conclusions about variation in extinction probability over time. Equation (7) has also been used in estimating λ as the slope of the $\ln N_t$ vs. t relationship. The constant λ assumption also yields the following expression for the expected lifespan, T , of subtaxa:

$$E(T) = 1/\lambda \quad (8)$$

(see derivations in Seber 1973:4; and Brownie et al. 1978: 203-204).

Some workers have estimated $E(T)$ as the average duration or interval between first and last encounter, and have then used (8) to solve for λ . Estimates of extinction probability based on (8) appear likely to be biased high in most situations.

The capture-recapture models that we suspect may be useful in paleobiological applications are summarized in Table 9. Here we specify the type of data needed, the quantities that can be estimated, and summary references for the models. Although these models are as yet unproven in paleobiological work, we believe that they will prove superior to methods currently used in estimating taxonomic diversity and extinction probabilities. This belief stems from the fact that, although these models do require assumptions which may prove restrictive, they permit relaxation of the following assumptions required by some current methodologies: (1) encounter probabilities all equal to 1.0, (2) encounter probabilities constant for all time periods, (3) extinction probabilities constant for all time periods.

Finally, we note that the use of capture-recapture models leads to various suggestions about the design of paleobiological sampling efforts. Many of these suggestions (e.g., various recommendations for reducing variation in encounter probability) have been made in the detailed discussions of model assumptions. In addition, for intensive studies of particular sites we recommend either the use of subsamples within a particular stratum or the tabulation of taxonomic frequency data (number of specimens per taxon) within strata. Either of these approaches will yield data which can be used to estimate taxonomic diversity in conjunction with closed population models and which thus follow Pollock's (1982) robust design. When compiling data of the type used to develop stratigraphic ranges, we recommend the recording of all

strata in which taxa are found. These additional encounters will provide a better data base for estimating extinction probabilities and will also permit estimation of numbers of total and new taxa, by stratum.

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Table 1. Expectations of the numbers of taxa encountered in stratum j and last encountered in stratum i , $E(a_{ij})$.

Stratum of last encounter (i)	Number taxa encountered	Stratum (j)			
		1	2	3	4
1	n_1		$n_1 \phi_1 p_2$	$n_1 \phi_1 \phi_2 (1-p_2) p_3$	$n_1 \phi_1 \phi_2 \phi_3 (1-p_2) (1-p_3) p_4$
2	n_2			$n_2 \phi_2 p_3$	$n_2 \phi_2 \phi_3 (1-p_3) p_4$
3	n_3				$n_3 \phi_3 p_4$

Table 2. Expectations of the numbers of taxa first encountered in geologic period i and encountered for the final time in period j , $E(R_{ij})$.

Period of first encounter	Number taxa encountered for first time	Stratum of final encounter		
		2	3	4
1	Q_1	$Q_1 f_2$	$Q_1 \phi_1 f_3$	$Q_1 \phi_1 \phi_2 f_4$
2	Q_2		$Q_2 f_3$	$Q_2 \phi_2 f_4$
3	Q_3			$Q_3 f_4$

Table 3. Gastropod species frequencies and encounter summary statistics for 5 well samples representing the Middle Miocene (from Sorgenfrei 1958).^a

Summary statistics ^b	Depth of well samples (m)				
	115	110-115	105-110	100-105	75-100
$f_{1,i}$	23	20	27	20	9
$f_{2,i}$	9	11	11	6	5
$f_{3,i}$	5	7	5	9	6
$f_{4,i}$	6	2	4	5	2
$f_{5,i}$	3	6	7	3	2
n_i	75	80	100	70	114
m_i	0	57	75	62	94
r_i	68	72	85	63	0
z_i	0	11	8	31	0

^aData are from Toftlund, Arnum formation.

^b $f_{j,i}$ = the number of species for which j specimens are found in sample i .
 n_i = the total number of species encountered in sample i . m_i = the total number of species encountered both in sample i and some previous (deeper) sample. r_i = the number of species encountered both in sample i and some more recent sample. z_i = the number of species encountered in earlier and more recent samples than i , but not in i .

Table 4. Estimates of species number, \hat{N}_i , survival rate, $\hat{\phi}_i$, and number of new species, \hat{B}_i , for the Sorgenfrei (1958) data on Gastropoda in well samples (Table 3).^a

Sample depth(m)	\hat{N}_i	$\hat{SE}(\hat{N}_i)$	$\hat{\phi}_i$	$\hat{SE}(\hat{\phi}_i)$	\hat{B}_i	$\hat{SE}(\hat{B}_i)$
115	100.8	7.7	0.92	0.02	7.0	9.7
110-115	100.0	6.3	0.92	0.02	38.3	10.2
105-110	129.8	8.2	0.88	0.02	5.0	18.3
100-105	119.4	16.5	-	-	-	-
75-100	123.0	4.2	-	-	-	-

^a \hat{N}_i and $\hat{SE}(\hat{N}_i)$ were estimated using model M_h (Burnham and Overton 1979), $\hat{\phi}_i$ and $\hat{SE}(\hat{\phi}_i)$ were estimated using the Jolly-Seber model, and \hat{B}_i and $\hat{SE}(\hat{B}_i)$ were estimated as in Pollock (1982).

Table 5. Jolly-Seber summary statistics for mammalian species from 12 samples (approximately 150-300 m) representing the Late Eocene record of the Big Horn Basin, Wyoming (from Schankler 1980).

Sample number ^b	Summary statistics ^a			
	n_i	m_i	r_i	z_i
19	31	0	29	0
18	25	22	24	7
17	33	26	32	5
16	6	6	6	31
15	34	28	31	9
14	8	7	6	33
13	25	23	21	16
12	15	13	11	24
11	36	25	28	10
10	28	27	21	11
9	13	13	11	19
8	31	30	0	0

^a n_i = the total number of taxa encountered in sample i . m_i = the total number of taxa encountered both in sample i and some previous (deeper) sample. r_i = the number of taxa encountered both in sample i and some more recent sample. z_i = the number of taxa encountered in earlier and more recent samples than i , but not in i .

^bEncounter data were taken from Schankler (1980:104-105, Fig. 3). We simply denoted the most recent sample as 1 and numbered consecutively as we proceeded to deeper samples.

Table 6. Jolly-Seber estimates of species number, \hat{N}_i , survival rate, $\hat{\phi}_i$, number of new species, \hat{B}_i , and encounter probability, \hat{p}_i , for the Schankler (1980) data on Late Eocene mammals (Table 5).

Sample number	Parameter estimates ^a						
	\hat{N}_i	$\hat{SE}(\hat{N}_i)$	$\hat{\phi}_i$	$\hat{SE}(\hat{\phi})_i$	\hat{B}_i	$\hat{SE}(\hat{B}_i)$	\hat{p}_i
19	-	-	0.94	0.02	-	-	-
18	33.1	1.4	0.96	0.02	7.3	1.9	0.75
17	39.2	1.6	0.97	0.01	0.0	1.4	0.83
16	37.0	0.0	1.00	0.03	7.8	1.9	0.16
15	45.7	2.3	1.00	0.22	4.2	7.6	0.74
14	55.6	13.3	0.81	0.16	0.6	6.2	0.14
13	45.4	3.3	1.00	0.15	5.1	4.9	0.55
12	51.4	8.4	0.79	0.11	13.1	5.2	0.28
11	53.7	4.8	0.85	0.07	0.0	3.3	0.66
10	43.0	3.0	0.82	0.09	0.0	0.8	0.65
9	35.2	3.3	-	-	-	-	0.37
8	-	-	-	-	-	-	-

^aEstimated with the bias-adjusted estimators of Seber (1973:204). Standard error estimates include only sampling variation.

Table 7. Numbers of invertebrate taxa first encountered in period *i* and last encountered in period *j*, Permian-Tertiary (from Raup 1978: Table 1).

Period of first encounter (<i>i</i>)	Number taxa encountered (Q_i)	Period of last encounter (<i>j</i>)			
		Triassic	Jurassic	Cretaceous	Tertiary
Permian	600	26	4	4	0
Triassic	937		84	45	6
Jurassic	1984			281	50
Cretaceous	2761				216

Table 8. Model 1 estimates of survival probability from Raup's (1978) Phanerozoic invertebrate data (Table 7).

Period (i)	Survival probability	
	$\hat{\phi}_i$	$\hat{SE}(\hat{\phi}_i)$
Permian	0.09	0.03
Triassic	0.33	0.05
Jurassic	0.31	0.05
Cretaceous	-	-

Table 9. Summary of capture-recapture models of potential use in analyzing specific types of paleobiological data.

Data type	Models	Estimable parameters and variables ^a	Summary references
Within strata, no sampling units, taxonomic presence-absence data	None available	-	-
Within strata, sampling units, taxonomic presence-absence data	M_o, M_t, M_h, M_{th}	N_i	Otis et al. (1978)
Within strata, no sampling units, taxonomic frequency data	M_h	N_i	Otis et al. (1978) Burnham and Overton (1979)
Several strata, taxonomic presence-absence data by stratum	Jolly-Seber	N_i, ϕ_i, B_i	Jolly (1965), Seber (1973)
Several strata, sampling units or taxonomic frequency data within strata	Robust Procedure	N_i, ϕ_i, B_i	Pollock (1982)
Several strata, taxonomic first and last encounter data	Model 1 (Band recovery)	ϕ_i	Brownie et al. (1978)

^aDemographic parameters and variables of primary interest are listed: N_i = total taxa in stratum i , ϕ_i = taxonomic survival probability for the period separating strata i and $i+1$, B_i = number of new taxa appearing during the period separating strata i and $i+1$ and extant at $i+1$.