ESTIMATING RATES AND PROBABILITIES OF ORIGINATION AND EXTINCTION USING TAXONOMIC OCCURRENCE DATA: CAPTURE-MARK-RECAPTURE (CMR) APPROACHES

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ABSTRACT.—We rely on observations of occurrences of fossils to infer the rates and timings of origination and extinction of taxa. These estimates can then be used to shed light on questions such as whether extinction and origination rates have been higher or lower at different times in earth history or in different geographical regions, etc. and to investigate the possible underlying causes of varying rates. An inherent problem in inference using occurrence data is one of incompleteness of sampling. Even if a taxon is present at a given time and place, we are guaranteed to detect or sample it less than 100% of the time we search in a random outcrop or sediment sample that should contain it, either because it was not preserved, it was preserved but then eroded, or because we simply did not find it. Capture-mark-recapture (CMR) methods rely on replicate sampling to allow for the simultaneous estimation of sampling probability and the parameters of interest (e.g. extinction, origination, occupancy, diversity). Here, we introduce the philosophy of CMR approaches especially as applicable to paleontological data and questions. The use of CMR is in its infancy in paleobiological applications, but the handful of studies that have used it demonstrate its utility and generality. We discuss why the use of CMR has not matched its development in other fields, such as in population ecology, as well as the importance of modelling the sampling process and estimating sampling probabilities. In addition, we suggest some potential avenues for the development of CMR applications in paleobiology.

INTRODUCTION

WHAT DRIVES changes in diversity and how fast diversity changes are key questions in paleobiology. Changes in diversity are proximately caused by extinction and origination, and immigration at more local scales. Here, we focus on the estimation of origination and extinction rates/probabilities while simultaneously taking into account the incompleteness in sampling. Although we allude to other methods for estimating origination and extinction rates using occurrence data where relevant, it is not our purpose here to thoroughly review other approaches.

Inference about diversity, origination and extinction would be relatively straightforward, given a complete record of taxonomic occurrence through time. In this case, applying methods from human demography to paleobiological data (Simpson, 1953; Kurtén, 1954; Van Valen, 1973; Raup, 1978) could be readily justified. Neither paleobiologists (Foote and Raup, 1996) nor population/community ecologists have complete data: we neither sample all individuals or taxa, nor all true births and deaths (originations and extinctions). Inference models that incorporate both the processes of ecological interest and the sampling processes that give rise to the data have a long history in ecology (Cormack, 1964; Williams et al., 2002; MacKenzie et al., 2006; Royle and Dorazio, 2008; Link and Barker, 2010) . One such approach and its relatives are variously known as capture-mark-recapture (CMR, the abbreviation we will use here), capture-recapture, mark-recapture and sight-resight methods. Although we don't "mark" taxa

as population ecologists mark individuals of a population, "marking" is analogous to "first observation" or "first appearance" while "recapturing" or "re-sighting" is analogous to subsequent observed occurrences after the "first observation" of a given taxon. The CMR philosophy of including both sampling and biological (and geological) processes in inference models is also appropriate for paleobiological data because sampling probabilities are never equal to 1, even under the best circumstances. Sampling probabilities in paleobiological questions include both preservation probability and the probability of fossil recovery, and we use sampling probability as such throughout this chapter. Related quantities are variously called sampling intensity or preservation rate (Foote, 2001; Peters and Ausich, 2008). Sampling probability is also termed detection or encounter probability in the CMR literature, and we use these interchangeably here. Although other methods have been independently developed to account for sampling probabilities, origination and extinction rates simultaneously (Foote, 2003; Alroy, 2008), they do not have the generality or convenience of CMR methods, as we will discuss at appropriate points later in the chapter.

Here we focus on use of CMR models, together with data on taxonomic occurrence from the fossil record, to draw inferences about taxonomic diversity and the associated rates of origination and extinction. We hope to demonstrate the general importance of modeling the sampling process and estimating sampling probabilities when studying paleobiological processes. To this end, we begin with the scenario in which we have a perfect fossil record. We then introduce the philosophy of CMR thinking and then transition into how one might model both the process of interest (e.g. extinction) and the sampling process. After listing the explicit assumptions of CMR, we discuss when various CMR assumptions are violated in paleobiological datasets and how to account for such violations. A very short overview of how one might estimate extinction and origination probabilities, as well as diversity and turnover probability, using CMR thinking, is given. Although we provide some examples in this chapter, we emphasize that this only serves as a starting point to delve into the world of CMR modeling. We highly recommend use of the annotated reading list at the end of this chapter in conjunction with the computational software recommended here and in the online supplement. In this chapter, we have chosen to adhere

to symbols and notations that are commonly used in the CMR literature, rather than to use notation found more commonly in the paleontological literature and hence in this volume for two reasons (see Table 1 for a summary of symbols used in this chapter). The first is to facilitate exploration of the original CMR literature after this brief introductory chapter, and the second is to emphasize that although we refer to commonly discussed processes such as extinction and origination, the parameters that we estimate are often different from those existing in a large part of the paleontological literature.

INFERENCES FOR COMPLETE RECORDS

For purposes of both defining the quantities of interest and motivating a CMR approach to modeling, we begin by considering how we might estimate these quantities of interest if the fossil record were perfect and complete. We also note that here we are considering global estimates given global data, although modifications can be made for regional or local data or temporally constrained data. For time-specific diversity, we would enumerate the taxa extant at given time intervals. We would similarly simply count the new taxa that are extant at one time interval and not in the previous interval to infer the number of originations. For inferences about extinction, we provide a simple numerical example.

Assume that 100 genera within a focal taxonomic group were extant at one time interval, and 20 of these were known to have gone extinct before a more recent time interval. Using this information, we could estimate the extinction probability for this group and time interval as $20/100 = 0.2$. If all 100 genera had similar a priori chances of going extinct in the interval, then 0.2 would be a good estimate of the probability that any randomly selected genus from the group would go extinct. In addition, 0.2 would be our best estimate of the expected fraction of genera extant at the earlier interval that went extinct during the interval. We view it as an expected fraction, because we are viewing the extinction process as probabilistic (if the process were repeated many times, we would be likely get different numbers of extinctions with each realization). We refer to this quantity as extinction probability in order to emphasize the underlying stochastic process, but

TABLE *1*.—List of (most of) the symbols as used in the text. Symbols are listed in the order of appearance in the text.

Symbol	Short verbal definition	Notes
t	Time interval or time	
p	Detection probability: probability that an extant taxon is detected by paleobiological sampling (synonym: encounter probability. Near synonyms: sampling probability, preservation probability)	p is related to the rate of preservation (commonly abbreviated as R) or sampling intensity commonly mentioned in the paleobiological literature. The standard symbol p is used in the CMR literature to represent detection probability, and it is usually simultaneously estimated with other parameters in the given CMR model. It is explicit in its definition that the taxa in question are truly present. We adhere to using p for detection probability, fully aware of its common use as "origination rate," to help the reader access the CMR literature more easily. In the text, we use the terms detection, encounter and sampling probabilities almost interchangeably, depending on the context.
$\hat{p}_t$	Estimated detection probability during time interval t	This is to illustrate that a "hat" over a symbol means that it is an estimate (or estimator) of the quantity of interest and a subscript refers to a particular instance when it is applied (e.g. time, a group of organisms or a particular facies).
S	True number of extant taxa	
s	Number of taxa encountered, found or observed	
ε_t	Extinction probability from t to $t+1$: probability that a taxon extant at t goes extinct before $t+1$	Note that q is the symbol usually used for extinction rates in the paleobiological literature.
m'_{t+1}	Number of taxa encountered at both t and $t+1$	Note that this is equivalent to Alroy's "two-timers" (Alroy 2008), although he calculates sampling probability differently.
M'_{t+1}	True number of taxa extant at t and still extant at $t+1$	
B_t	True number of newly originating taxa between t and $t+1$	
γ_t	Complement of turnover: the probability that a randomly selected taxon extant at t did not originate between t-1 and t	The probability that a randomly selected taxon extant at t, originated between t-1 and t. This is one way of formulating origination probability, usually symbolized as p in the paleobiological literature.
U_t	The number of taxa extant at t which had not been encountered prior to t	
u_t	The number of taxa first encountered in t (which had not been encountered prior to t)	
M_t	The number of extant taxa that have been encountered before t	
λ_t	Rate of change in taxon richness	Estimated as $\hat{S}_{t+1} / \hat{S}_t$
f_t	Per taxon rate of origination	Estimated as $\hat{B}_t / \hat{S}_t$

we recognize that the paleobiological literature also refers to related concepts including "extinction rate," "per-taxon extinction rate" and "extinction intensity" (Raup and Boyajian, 1988; Pease, 1992; Foote, 1994; Alroy, 2000; Wagner et al., 2007). Another quantity of interest is "turnover". This term has been defined in many different ways, but we define it probabilistically as the probability that a taxon extant in some time interval is new, in the sense that it was not extant the previous time interval (Nichols et al., 1986). This definition of turnover is also equivalent to the expected fraction of species present in a time interval that are new (originated since the previous time interval). Turnover is then estimated by dividing the number of new taxa in a time interval by the total number of extant taxa for that interval.

INCOMPLETE RECORDS AND CMR THINKING

Records of taxonomic occurrence are not complete, though, and a taxon extant at one time interval may not be identified from the fossil record of that time interval. Thus, we will consider encounter histories for individual taxa as strings of 0's and 1's, with 1 indicating that the taxon was detected in a time interval and 0 indicating no detection. Thus, the encounter history for a specific genus over 8 time intervals might be: 0 0 1 0 1 1 0 0, with each entry corresponding to a specific time interval. This genus was not observed in interval 1 or 2, it was first detected in interval 3 (i.e. it was "marked") and then again in intervals 5 and 6, and never observed after interval 6. Despite the incompleteness of the record, there are some things of which we are certain, assuming no major data errors or major reworking of fossils. The taxon originated some time prior to or during interval 3, and it was extant and contributed to the diversity of intervals 3-6. We also know that the taxon did not go extinct prior to interval 6. Although we might strongly believe that the taxon is unlikely to have survived long after interval 7 (imagine for instance, a very long string of zeros after interval 6), we still do not know whether or when it became extinct after interval 6, given that encounter probability (i.e. the combined probabilities of preservation and of fossil recovery) is never 1.

So the typical encounter history provides only limited information about time-specific diversity, originations, extinction and turnover. In order to be able to draw strong inferences about these quantities of biological interest, we must know something about the sampling process that also contributed to this history. Luckily, a history such as this does provide information about encounter or detection probability, the probability that at least one representative of a taxon is encountered and identified for a specific time interval, conditional on the taxon being extant at that time. For every taxon in the group of interest that is encountered in more than one time interval over a specified range of geologic time, we can condition on the time intervals of first and last encounter as a means of providing a subset of data for which we know truth. Specifically, we know that for each time interval between first and last encounter, the taxon was extant. This knowledge provides us with a simple way to estimate encounter probability. We can take any time interval, t, determine how many taxa in our set of interest were known to be extant then (known because they were encountered at times before t and after t), and then ask how many of these were encountered at t. The number encountered at t, divided by the number known to be extant at t, estimates detection probability, p_t, for interval t. As an example, the data set of Table 2 consists of hypothetical encounter histories for 20 taxa across 8 time intervals. Let's consider the estimation of detection probability for interval 6. We begin by conditioning on encounter histories that include encounters before and after interval 6; specifically histories for taxa A, E, F, G, I, K, N, O, R, and S. We then see that 5 of these taxa (F, G, I, O, R) were encountered during interval 6, so

$$\hat{p}_6 = 5/10 = 0.5 .$$

The "hat" on p simply indicates that this is an estimate for p. Note that an estimator is a function of the observed data while an estimate is the number that results from the application of this function to a sample of data. We will be using the "hat" to denote both estimates and estimators throughout the text.

Armed with estimates of time-specific detection probabilities, we can now draw inferences about the quantities of biological interest. For example, we can estimate total number of taxa in interval t (denote as S_t) by dividing the number of taxa encountered in that time interval, s_t, by the detection probability, $\hat{p}_t$, corresponding to that interval. For the data of Table 2,

TABLE 2.—Encounter histories of taxa A through T.

Taxon	Time interval							
	1	2	3	4	5	6	7	8
A	0	0	1	1	0	0	1	0
B	0	1	0	0	0	0	0	0
C	0	0	0	0	0	1	1	1
D	1	0	1	1	0	1	0	0
E	0	0	0	1	0	0	1	1
F	0	1	0	0	1	1	0	1
G	0	0	0	1	0	1	1	0
H	0	0	0	0	0	1	1	0
I	0	0	1	0	1	1	0	1
J	1	0	0	0	0	0	0	0
K	0	0	0	0	1	0	1	1
L	0	0	1	1	0	0	0	0
M	0	1	0	1	1	0	0	0
N	1	1	0	0	1	0	1	0
O	0	0	0	1	0	1	1	1
P	0	0	1	0	0	0	0	0
Q	0	0	0	0	0	0	1	0
R	0	0	1	0	1	1	0	1
S	0	0	0	0	1	0	0	1
T	0	0	0	1	0	0	0	0

we can estimate the number of taxa for interval 6 as:

$$\hat{S}_6 = s_6 / \hat{p}_6 = 8 / 0.5 = 16$$

We can estimate extinction probability, ε_t, for t to $t+1$ [which we can also denote as $(t, t+1)$], by conditioning on the number of taxa encountered at interval t, and asking how many of these are still extant at $t+1$. Denote the number of taxa encountered at both times, t and $t+1$, as m'_{t+1}. We can then estimate the number of those taxa encountered at t that are still extant at $t+1$, M'_{t+1}, as:

$$\hat{M}'_{t+1} = m'_{t+1} / \hat{p}_{t+1} \qquad (1)$$

Extinction probability is then estimated as the complement of the ratio of $t+1$ survivors to encounters at t.

$$\hat{\varepsilon}_t = 1 - (\hat{M}'_{t+1} / s_t) \qquad (2)$$

We estimate extinction by using survivors rather than non-survivors because we observe survivors (albeit incompletely), but not non-survivors. More specifically, when we observe a taxon to have survived, "truth" is known for this taxon, whereas "truth" is never known for taxa that are not observed again (at any interval, they may be extinct, or they may be extant but not detected). Returning to Table 2, we can estimate extinction probability for interval 5 to interval 6 as:

$$\hat{\varepsilon}_5 = 1 - (\hat{M}'_6 / s_5) = 1 - \frac{3/0.5}{7} \approx 0.14.$$

Inference about origination requires estimates of total taxa for 2 successive time intervals and of extinction between the 2 intervals. For example, in order to estimate the number of taxa originating between time intervals 5 and 6 and extant in interval 6, we first need to estimate number of taxa extant in interval 5. We do this by estimating detection probability for interval 5, which is $\hat{p}_5 = 4/9 \approx 0.4$, because there were 9 encounter histories that show encounters both before and after interval 5 (taxa A, D, E, F, G, I, N, O, R), 4 of which have detections in interval 5 (F, I, N, R). The estimated number of taxa extant in interval 5 is then:

$$\hat{S}_5 = s_5 / \hat{p}_5 = 7 / 0.44 \approx 16.$$

We then estimate the number of taxa originating between intervals t and $t+1$ (denote as B_t) as:

$$\hat{B}_t = \hat{S}_{t+1} - \hat{S}_t(1 - \hat{\varepsilon}_t) \qquad (3)$$

Equation 3 is based on the fact that taxa extant at time $t+1$ are comprised of two groups, survivors from the previous interval, t, and new taxa that originated between t and $t+1$. We can estimate the expected number of taxa extant at t that survive to $t+1$ as $\hat{S}_t(1 - \hat{\varepsilon}_t)$. Subtracting the expected number of survivors from diversity at $t+1$ then yields an estimate of taxa originating during $(t, t+1)$. Based on the data of Table 2, we can estimate B_5, the number of taxa originating between intervals 5 and 6, as:

$$\hat{B}_5 = \hat{S}_6 - \hat{S}_5(1 - \hat{\varepsilon}_5) = 16 - 16(0.86) \approx 2.$$

We can define a parameter, γ_t, as the probability that a randomly selected taxon extant at t is "old" (i.e., did not originate between $t-1$ and t). Thus, $1 - \gamma_t$ is turn-

over, the probability that a randomly selected taxon at t originated between t-1 and t. Based on the above estimates, we can estimate turnover as:

$$1 - \hat{\gamma}_t = \hat{B}_{t-1} / \hat{S}_t \qquad (4)$$

For the data of Table 2, turnover for interval 6 can be estimated as:

$$1 - \hat{\gamma}_6 = \hat{B}_5 / \hat{S}_6 \approx 2/16 \approx 0.13 .$$

Thus, using intuitive computations, we can estimate quantities of interest from encounter history data, even though these data are incomplete and are characterized by encounter probabilities that are less than 1. Finally, we can also modify equation 4 and estimate per-taxon origination rate, defined as new taxa at t+1 per old taxon at t, as $\hat{B}_t / \hat{S}_t$ (Connolly and Miller, 2001b).

INCOMPLETE RECORDS AND CMR MODELING

Although the above estimators are approximately unbiased for large sample sizes, they are inefficient and are presented here only to illustrate the intuition that underlies CMR inference. Efficient estimation is based on formal inference methods; usually either maximum likelihood or Markov chain Monte Carlo (MCMC) (Royle and Dorazio, 2008; Link and Barker 2010; Wang, this volume). Both of these approaches require explicit models for the processes (sampling and biological) that generate the taxonomic encounter history data. These probabilistic models must include the parameters of biological interest (e.g., ε_t), as well as parameters associated with the sampling process (p_t). The history of CMR modeling, and of our own experience with such modeling, has been based largely on likelihood approaches to inference, so we will primarily focus on these approaches here. However, we remind the reader that MCMC approaches are also useful for these models and actually permit implementation of certain kinds of models (e.g., with individual random effects) that would be very difficult to implement via any other approach (Link and Barker, 2005, 2006; Royle and Dorazio, 2008; Link and Barker, 2010).

CONDITIONAL MODELS FOR INFERENCE ABOUT EXTINCTION

To begin, we simplify the modeling by focusing only on inference about extinction. Such inference is typically accomplished by conditioning on the initial encounter of each taxon. Consider the following encounter history for a taxon: 0 0 1 0 1 1 0 0. When we condition on the initial encounter in interval 3, we do not have to model the initial "0 0 1" of the record, instead using the "1" in interval 3 as a starting point. The model for this history can thus be written as follows:

$\text{Pr}(0\ 0\ 1\ 0\ 1\ 1\ 0\ 0\ |\quad$ initial encounter in interval 3$) =$

$$\begin{aligned} &(1 - \varepsilon_3)(1 - p_4)(1 - \varepsilon_4)p_5(1 - \varepsilon_5)p_6 \times \\ &[\varepsilon_6 + (1 - \varepsilon_6)(1 - p_7)\{1 - (1 - \varepsilon_7)p_8\}] \end{aligned} \qquad (5)$$

Beginning with the encounter of this taxon in interval 3, it survived to interval 4 (with probability, $1 - \varepsilon_3$), was not encountered then $(1 - p_4)$, survived to interval 5 $(1 - \varepsilon_4)$, was encountered in interval 5 (p_5), survived until interval 6 $(1 - \varepsilon_5)$, was encountered in interval 6 (p_6) and was never encountered after interval 6. Several possible events could have resulted in the failure to encounter the taxon following interval 6. It could have gone extinct between intervals 6 and 7 (ε_6), or it could have survived from interval 6 to 7 $(1 - \varepsilon_6)$, not been detected in interval 7 $(1 - p_7)$, followed by not surviving, or surviving but not being encountered, in interval 8 $\varepsilon_7 + (1 - \varepsilon_7)(1 - p_8)$, which simplifies to $[1 - (1 - \varepsilon_7)p_8]$. This latter probability is simply a shorthand way of combining the probability that the taxon went extinct between intervals 7 and 8 and the probability that the taxon did not go extinct, but was not encountered in interval 8.

Formal parameter estimation by methods such as maximum likelihood and MCMC is based on two essential components: (1) a set of data and (2) models of the processes that generated the data. In the specific case of trying to estimate extinction probability from the fossil record, the data are the encounter histories for every taxon in the group of interest over the time interval of interest, e.g., as in Table 2. In a maximum likelihood framework, we would multiply the probabilities of the encounter histories of all the taxa in the dataset, given a model, and then search for ε's and p's that maximize this likelihood function (Wang, this

volume). One possible model for these data is that used to model the example encounter history above. We might denote that model as (ε_t, p_t), indicating that there is time-specificity of both extinction and encounter probabilities, that is, both extinction and sampling probabilities are allowed to take on different values at different time intervals during the estimation. Alternative models might restrict extinction probability to be constant over time, such that extinction over any time interval would be modeled as

$$\varepsilon_t = 1 - (1 - \varepsilon')^{\Delta t} \qquad (6)$$

where ε_t is the probability that the taxon goes extinct during the interval $(t, t+\Delta t)$, and ε' is the probability of going extinct per unit time, expressed in the same time units as Δt, the time interval to which the extinction probability, ε_t, corresponds. A model with extinction constant over time and encounter probability time-specific would be written as $(\varepsilon., p_t)$, with the dot indicating time-constancy. In this case, the model represents a scenario in which the variation in the data comes solely from varying detection through time, and extinction probabilities are not changing at all. For each model, estimation of model parameters requires the encounter history for each taxon and the probability associated with that history, based on the model (see Lebreton et al. 1992, Williams et al. 2002).

With the CMR approach, we can easily consider models in which basic model parameters such as extinction and encounter probabilities are themselves modeled as functions of covariates. The covariates may be time-specific, corresponding to specific time intervals, or they may be taxon-specific. For example, either body size or diet (e.g., carnivore, omnivore, herbivore) might be a taxon-specific covariate that would express a biologically-interesting hypothesis about vulnerability to extinction (Liow et al., 2008), while global productivity could be a time-specific covariate for originations (Connolly and Miller, 2002). Covariate modeling of encounter probabilities would involve potential sources of variation in these sampling probabilities. For example, a time-specific covariate for encounter probabilities might be, say, rock volume or estimated sedimentation rates, while a taxon-specific covariate might be say aragonite or calcite shells (Kidwell and Holland, 2002) . A common approach to covariate modeling with CMR data uses logistic modeling, for example,

$$p_{i,t} = \frac{e^{\beta_0 + \beta_1 x_i + \beta_2 y_t}}{1 + e^{\beta_0 + \beta_1 x_i + \beta_2 y_t}} \qquad (7)$$

where x_i is a taxon-specific covariate for taxon i, y_t is a time-specific covariate for time t, the β's are parameters to estimate, and $p_{i,t}$ is the encounter probability for taxon i at time t. Logistic modeling provides a natural framework for modeling probabilities, which assume values between 0 and 1, as functions of continuous or categorical covariates. Information about the factors affecting encounter probabilities and those affecting origination and extinction probabilities can be included in models we wish to compare [e.g. using the Akaike Information Criterion (Akaike, 1973)]. Estimates of the various probabilities from different models can also be compared or even averaged across models if desired (Burnham and Anderson, 2002).

As with all estimation models and associated estimators, the basic conditional modeling of extinction probability described above is based on simplifying assumptions about the sampling and biological processes that generated the data. Developers of CMR models have historically been careful to present assumptions explicitly and have also investigated the consequences of violating these assumptions (Pollock et al., 1990; Williams et al., 2002). The earliest CMR model suitable for inference about global extinction probabilities is the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965), model (ε_t, p_t) described above.

Assumptions underlying the CJS model, as applied to taxonomic occurrence records, are (e.g., (Williams et al., 2002)):

1) After initial encounters, encounter probabilities for all taxa in the group of interest are equal, $p_{i,t} = p_t$ for all taxa, i;

2) After initial encounters, extinction probabilities for all taxa in the group of interest are equal, $\varepsilon_{i,t} = \varepsilon_t$ for all taxa, i;

3) Sampling intervals are short relative to the time over which extinction is to be estimated;

4) The fate of each taxon with respect to extinction and encounter is independent of the fate of every other taxon.

In addition, we assume (as in most other paleontological methods that rely on taxonomy and age models) that specimens are correctly identified (i.e. species A is identified as species A and not mistaken as species B) and that there are no major reworkings of specimens or temporal miscorrelations (i.e., Ordovician fossils are not reworked into Oligocene rocks and a Pliensbachien sample is not mistaken as a Pliocene sample).

CMR may seem exceedingly restrictive at this point, but we emphasize that most other approaches to inference require even more restrictive assumptions, although they are not commonly articulated. Indeed, strengths of CMR are that the assumptions are made explicit and there are many well developed ways to relax them. More importantly, methods that ignore encounter probabilities can be shown to yield biased estimates and may also give false confidence to one's conclusions.

Assumptions 1 and 2 can be relaxed by using taxon-specific covariates that permit variation among taxa in encounter and extinction probabilities. For example, trilobites, brachiopods and gastropods all have high preservation potentials, but brachiopods probably preserve better than trilobites which in turn probably preserve better than many gastropods. These three groups probably also have different environmental preferences and these various environmental settings may have different preservation qualities over time. We also suspect that extinction rates for trilobites had probably been very high, for example with respect to most brachiopods (Gilinsky and Good, 1991). In the CMR approach, we can model these differences with ease. For example, we can set up our models such that all three groups have the same encounter and/or extinction probability or such that each has a different probability. In the first case, there will be fewer parameters to estimate while in the latter, there are more. The process of model selection then attempts to focus on a parsimonious model that represents a compromise between good fit and small number of parameters (Burnham and Anderson, 2002). In a similar vein, if the idea is that the type of environment dominating during a given time interval is thought to influence preservation from time interval to time interval, e.g. aragonitic versus calcitic environments (Cherns and Wright, 2009), we can easily model preservation using preservation environments as covariates. Even if we may not know what covariates to include or may not have information on potential covariates, inference about extinction probabilities is typically robust to unmodeled variation in encounter probabilities (Carothers, 1973, 1979; Pollock et al., 1990).

Records of fossil occurrences are often based on correlating deposits and thus tend to assign records to large time intervals, hence assumption 3 is regularly violated in paleontology. A particularly striking example is the rapid rate of trilobite genera extinction (Foote, 1988) where few genera manage to last the length of a standard PBDB (paleobiology database http://www.paleodb.org) time bin. However, investigations of the consequences of violating this assumption suggest that this does not constitute a severe problem (Smith and Anderson, 1987; O'Brien et al., 2005) and that estimates of extinction probabilities will still be reasonable, recognizing that they extend from the approximate mid-point of one time interval to the approximate mid-point of the next (Nichols and Pollock, 1983; Conroy and Nichols, 1984; Nichols et al., 1986). Note that although this assumption is typically stated by users of CMR models, it is relevant to any approach to estimating survival or extinction for entities identified as alive/extant only to a specified time interval rather than to an instant in time.

Assumption 4 might also be important for specialist taxa, for example, a specialist predator that was only likely to be found in the same locations as a specific prey taxon, possibly leading to dependent encounter probabilities. In this case, estimates of extinction probabilities should not be biased, although corresponding variance estimates may be too small. There are also ways to correct variance estimates for violations of assumption 4 (overdispersion), but we have to discuss goodness-of-fit tests before we can explain this with ease. The process of fitting and selecting CMR models typically begins with goodness-of-fit testing for the most general model in the set of considered models (Burnham and Anderson, 2002; Williams et al., 2002). Among conditional models for extinction estimation, the model (ε_t, p_t) is very general, and goodness-of-fit tests have been developed for it and automated (Pollock et al., 1985; Burnham et al., 1987).The goodness-of-fit test statistics are asymptotically distributed as χ^2, and a variance inflation factor, $\hat{c}$, can be computed as $\hat{c} = \chi^2/df$, where df is the degrees of freedom associated with the χ^2 test statistic. Model-based variance estimates are multiplied by the variance inflation factor $\hat{c}$ in order to obtain corrected variance estimates. In

addition, AIC statistics can be corrected to produce a quasi-likelihood statistic, QAIC, modified to deal with over-dispersion (e.g., Burnham and Anderson 2002). For more details on this general approach and on specific approaches to goodness-of-fit that rely on Monte Carlo simulation, rather than asymptotics, we refer the reader to synthetic treatments and practical guides (Burnham and Anderson, 2002; Williams et al., 2002; Cooch and White, 2006).

In addition to providing good estimates of parameters and associated variances, formal approaches to inference such as maximum likelihood and MCMC have other advantages (see Wang, this volume for details). For example, likelihood approaches permit direct tests between competing models (likelihood ratio tests) and computation of model selection statistics such as Akaike's Information Criterion (Akaike, 1973; Lebreton et al., 1992; Burnham and Anderson, 2002; Williams et al., 2002). Model selection approaches for Bayesian inference include the deviance information criterion and reversible jump MCMC (Link and Barker, 2006; Royle and Dorazio, 2008; Link and Barker, 2010).

UNCONDITIONAL MODELS FOR INFERENCE ABOUT DIVERSITY, ORIGINATION, TURNOVER

Conditional models for inference about extinction and encounter probabilities thus begin with the initial encounter of a taxon and then model the subsequent encounter history data. Inferences about origination focus as well on the initial encounters of taxa and thus require a model for the processes that produce encounters of taxa that have not been previously encountered. The original Jolly-Seber approach (note that is different from the CJS approach described earlier, which is conditioned on initial encounters) begins by defining an unknown random variable, U_t, corresponding to the number of taxa extant at time t that have not been encountered prior to time t. From the conditional modeling described above (i.e., the CJS model), we know how to estimate the encounter probability (p_t) associated with taxa that have been previously encountered. If this encounter probability also applies to taxa not yet encountered, then we can estimate the number of such taxa as

$$\hat{U}_t = u_t / \hat{p}_t \qquad (8)$$

where u_t is the number of taxa first encountered in time t. However, the number of taxa at any time that has not yet been encountered (U_t) is perhaps not a particularly interesting quantity. Rather, we would like to know how many new taxa actually originated between t and $t+1$ and are available to be encountered at $t+1$, B_t. Such inference requires estimates of total taxa, S_t.

Diversity or number of extant taxa in the group of interest can be written as the sum of extant taxa that have been encountered prior to t (M_t) and extant taxa that have not been previously encountered: $S_t = M_t + U_t$. Incomplete encounter data do not provide direct counts for any of these quantities, but the ability to estimate encounter probability allows us to estimate S_t as:

$$\hat{S}_t = \hat{M}_t + \hat{U}_t = m_t / \hat{p}_t + u_t / \hat{p}_t = s_t / \hat{p}_t \qquad (9)$$

We can now estimate the number of taxa originating between times t and $t+1$ (i.e., $\hat{B}_t$) by plugging $\hat{S}_t$ from equation 9 into equation 3. Finally, turnover, the probability that a randomly selected taxon extant at $t+1$ is new (was not extant at t) can be estimated as:

$$1 - \hat{\gamma}_{t+1} = \hat{B}_t / \hat{S}_{t+1} \quad \text{(see equation 4)}$$

By treating the number of new taxa, B_t, as a random variable, the unconditional Jolly-Seber approach described above focuses on the sampling process and p_t, but provides no direct opportunity for modeling the biological process of origination, at least within the model structure. Newer, alternative approaches to modeling origination data do provide such opportunities and merit brief discussion here. When encounter data are viewed in reverse time order (from last encounter to first encounter), conditional modeling provides information about the recruitment or origination process (Pollock et al., 1974). Specifically, the encounter history data are written in reverse time order and modeled with encounter and turnover probabilities rather than encounter and extinction probabilities. Consider the encounter history, 0 0 1 0 1 1 0 0, used above as an example of conditional modeling for inference about extinction. Under the reverse-time approach (Pradel, 1996), this history is modeled as follows:

Pr(0 0 1 0 1 1 0 0 | final encounter in interval 6) =

$$\gamma_6 p_5 \gamma_5 (1 - p_4) \gamma_4 p_3 [(1 - \gamma_3) + \gamma_3 (1 - p_2)(1 - \gamma_2 p_1)] \quad (10)$$

Beginning with the final encounter at time 6, we know that the taxon did not originate between 5 and 6 (we know this because the taxon was encountered in previous time intervals), and the probability associated with this event is γ_6. The taxon was encountered in interval 5 (p_5), it did not originate between 4 and 5 (γ_5), it was not detected at time 4 ($1 - p_4$), it did not originate between time intervals 3 and 4 (γ_4), and it was encountered in interval 3 (p_3). The final term in brackets includes the possibility that the taxon originated between intervals 2 and 3($1 - \gamma_3$), as well as the possibility that the taxon did not originate between intervals 2 and 3 (thus was extant at 2) and was not encountered in 2 $[\gamma_3(1 - p_2)]$, and that it either originated between 1 and 2 or was extant at 1 but not encountered, i.e., $(1 - \gamma_2) + \gamma_2(1 - p_1)$, which simplifies to $(1 - \gamma_2 p_1)$. This conditional approach can be used to estimate turnover and encounter probabilities directly.

Pradel combined the standard-time and reverse-time approaches in a single unconditional likelihood (Pradel, 1996), sometimes referred to as the temporal symmetry approach (Williams et al., 2002). This approach permits simultaneous estimation of parameters associated with extinction (ε_t), the complement of turnover (γ_t), and encounter probability (p_t). Total extant taxa, S_t, is estimated as under the Jolly-Seber approach described above, and number of taxa originating between t and $t+1$ can be estimated as (equation 4):

$$\hat{B}_t = (1 - \hat{\gamma}_{t+1})\hat{S}_{t+1} .$$

Pradel (1996) described different parameterizations of this model that may be useful, depending on the biological questions of primary interest. One parameterization permits direct estimation and modeling of rate of change in diversity between 2 successive time intervals, $\lambda_t = S_{t+1}/S_t$. The other parameterization permits direct estimation and modeling of newly-originated taxa extant at $t+1$, per taxon extant at t, $f_t = B_t/S_t$. In the paleobiological context, this parameter, f_t , also can also be viewed as a per taxon rate of origination (read also text around equation 4).

Another modeling approach that is used in animal ecology is known as the superpopulation approach (Crosbie and Manly, 1985; Schwarz and Arnason, 1996). This approach begins by defining a superpopulation, S. In the paleobiological context this quantity represents the total number of taxa extant, and thus available to be encountered, at some time during the entire time interval of interest:

$$S = \sum_{t=0}^{K-1} B_t ,$$

where we assume that the time intervals for which encounter history data are being considered range from 1 (oldest interval) to K (most recent interval) . The B_t are viewed as multinomial random variables with corresponding probabilities, β_t, representing the probability that a member of the taxonomic super-population, S, originated between times t and $t+1$. The probability β_0 is defined as the probability that a member of N is extant at the very first sampling interval, 1. Thus, conditional on the set of taxa extant at some time during the interval under consideration $(1, K)$, the β_t represent time-specific probabilities of origination. The superpopulation modeling approach also includes as parameters the probabilities of extinction, ε_t, and encounter, p_t, described previously.

These unconditional approaches that extend inference beyond probabilities of encounter and extinction to taxonomic diversity, origination and turnover, require all of the assumptions listed above for the conditional modeling of extinction and encounter probabilities. In addition, the unconditional approaches require the assumption that encounter probabilities for taxa encountered during previous intervals apply similarly to taxa that have not been encountered previously (i.e., p_t applies to U_t as well as to M_t).

COMPUTATIONS, SOFTWARE AND EXAMPLES

Various computer programs have been written to conduct CMR analyses, but rather than provide a catalog of these, we simply point paleobiological users at this time to the freely available program MARK (White and Burnham, 1999) and its accompanying online book (Cooch and White, 2006) which we highly recommend. The Cooch and White (2006) book is much more than a user's manual, as it provides not only instructions on program use, but is also an excellent introduction to the models and methods themselves. Given that many paleobiologists are R users, we note that there is an R package (RMark by Jeff Laake and Eric Rexstad) which is an alternative interface for MARK which makes the construction of models less cumbersome (note that MARK has to be installed for RMark to work). In the

online supplement to this chapter, we walk the reader through the analyses of a couple of example data sets.

CLOSING REMARKS

The use of CMR thinking and modeling was first introduced in the paleontological literature in the 1980s by statistical ecologists who realized that the methods that they were developing in ecology could benefit paleontologists (Nichols and Pollock, 1983; Conroy and Nichols, 1984; Nichols et al., 1986). However, the CMR approach was only used very sporadically in the paleontological literature following those papers (Connolly and Miller, 2001a, 2001b, 2002; Chen et al., 2005; Kröger, 2005; Liow et al., 2008). We think there are several reasons for this. The first is that the explicit assumptions for CMR may seem too strict, but we have explained the benefits of these explicit assumptions and suggested ways for getting around them. We also believe that the failure to specify assumptions underlying ad hoc methods may lead readers to the false conclusion that these methods are less restrictive. However, in reality the assumptions underlying ad hoc approaches to inference typically include all of those required by CMR models as well as additional restrictive assumptions about the sampling process. The second is that the terminology used in CMR approaches, largely derived from the population ecological literature, is not easily "translated" into paleontological interpretation, but we hope that we have given a good introduction to both the philosophy and terminology behind CMR. Third, we have only recently begun to compile large datasets of occurrence records, so the wide application of modern CMR approaches had not been possible earlier (note though that band recovery models had been applied to first and last appearance data, e.g. Nichols and Pollock 1983; Conroy and Nichols 1984). We hope that this chapter encourages greater enthusiasm for this flexible and powerful approach.

Sampling incompleteness or non-detection is not a statistical fine point, but instead can cause serious biases in estimators that ignore this issue (e.g., Pollock et al. 1990, Williams et al. 2002, MacKenzie et al. 2006). It is also clear from the paleobiological literature that incomplete sampling must be included in models of origination, extinction and turnover (Alroy et al., 2001; Foote, 2003). Although not accounting for preservation incompleteness may give reasonable results sometimes

(Foote, 2001, 2003), there is never a guarantee of this. Substantial bias is always possible. Without going through the exercise of incorporating preservation and sampling probabilities into our inference methods, we cannot know if the estimates for origination and extinction probabilities using methods that ignore preservation and sampling are reliable, despite continued use of methods that treat observed data as though they reflect complete detection to calculate extinction and origination rates (Krug et al., 2009; Stanley, 2009). We need to begin to account for incomplete sampling in our models. Standardization may alleviate some problems of uneven sampling (Alroy et al., 2001; Alroy et al., 2008), but standardization necessarily involves sources of variation in detection processes that we can identify and control. Unfortunately, there are many likely sources of variation that we cannot identify and control. Preservation rates are sometimes estimated independently and then applied to fossil encounter data in a second analysis (Barry et al., 2002). Once again, encounter probabilities are influenced by a variety of factors, including preservation rates, various sampling issues, abundance of individuals of each focal taxon through time, etc. Rather than trying to identify all of these factors and then somehow deal with them (or sometimes not), it seems much more reasonable to use analytic methods that include encounter probabilities that can vary over time and possibly taxon, and to include these directly in our modeling.

Because occurrence data in paleobiology are becoming more and more common as already mentioned, we have framed this introduction using "encounter history data," (the analogue for occurrence data in ecology). We note however, that there are also inference approaches that should be useful for first and last occurrence only data (Conroy and Nichols, 1984; Brownie et al., 1985). In addition, the models presented above provide natural approaches for estimating confidence intervals for stratigraphic ranges, another topic of interest to paleobiologists (Marshall, this volume).

In addition to inferences about global diversity, extinction and origination, other ecological methods that deal with sampling or non-detection issues would seem to have great potential for addressing other paleobiological questions. For example, within a time interval, we might be interested in taxonomic diversity associated with different geographic locations. Multiple samples from a specific location permit inference about

taxa missed, and thus total taxa extant, using either CMR (Otis et al., 1978; Nichols and Pollock, 1983; Williams et al., 2002) or occupancy modeling (MacKenzie et al., 2002; MacKenzie et al., 2006) approaches. Inference about geographic range of a taxon at a specific time interval can be obtained from data that include multiple samples at multiple geographic locations (MacKenzie et al., 2002; MacKenzie et al., 2006). Similarly, inference about local rates of extinction and colonization of a taxon can be based on multiple samples at each of multiple geographic locations across multiple time intervals using models for occupancy dynamics (MacKenzie et al., 2003; MacKenzie, 2006). This list is not exhaustive, but is simply provided to indicate the potential of the explicit modeling approaches similar to that presented in this paper.

ANNOTATED READING LIST

All three books are cited in the chapter.
1) BURHAM, K. P., AND D. R. AANDERSON. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach.

This book explains how to select the best model(s) based on the data one has on hand. Model formulation and selection are important components of the CMR approach, and Burnham and Anderson give a highly readable introduction to these topics.

2) COOCH, E., AND G. WHITE. 2006. Program Mark: A Gentle Introduction (http://www.phidot.org/software/mark/docs/book/).

This is a free online volume that gives a step by step introduction to the program MARK, a comprehensive package that runs CMR models. But in addition to being a guide to MARK, it also explains a lot of the workings of CMR. Best of all, since it is downloadable as a pdf, it is searchable.

3) WILLIAMS, B. K., J. NICHOLS, AND M. J. CONROY. 2002. Analysis and Management of Animal Populations.

Even though this book is written for population ecologists, a few chapters are highly relevant to the issues and concepts we have discussed in this chapter. Particularly relevant are chapters 2, 3, 14, 16-20.

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