VIII. **Inverse procedure**: Use of time-varying models to estimate true time series of \( p \), \( q \), and \( r \).

**A. Basic approach**

1. Tabulate number of taxa, \( X_{ij} \), with first appearance in interval \( i \) and last appearance in interval \( j \); intervals numbered from 1 to \( n \).

2. For candidate parameter vectors \( \vec{p}, \vec{q}, \) and \( \vec{r} \) \((\vec{p} = (p_1, p_2, ..., p_n) \) etc.), use branching and sampling model to predict \( P_{\rightarrow ij} \), the probability that a taxon with first appearance in \( i \) will have a last appearance in \( j \), and \( P_{\leftarrow ij} \), the probability that a taxon with last appearance in \( j \) will have a first appearance in \( i \).

3. **Likelihood function**:

\[
L = \prod_{i=1}^{n} \prod_{j=i}^{n} P_{\rightarrow ij}^{X_{ij}} \times \prod_{j=1}^{n} \prod_{i=1}^{j} P_{\leftarrow ij}^{X_{ij}},
\]

where \( n \) is the number of time intervals. The corresponding support (log-likelihood) is:

\[
S = \ln(L) = \sum_{i=1}^{n} \sum_{j=i}^{n} X_{ij} \ln(P_{\rightarrow ij}) + \sum_{j=1}^{n} \sum_{i=1}^{j} X_{ij} \ln(P_{\leftarrow ij}).
\]

4. Numerically explore the \( (\vec{p}, \vec{q}, \vec{r}) \) parameter space to find the set of values that maximizes the likelihood (support) for a given dataset.


- Tests like these are generally worth carrying out whenever a new method is being approached.

1. **Internal consistency**

   a. Simulate first and last appearances using known parameters, and *in a way that agrees with the model*; check whether parameters can be recovered. (Foote 2001, Figs. 1-4)

   b. Artificially degrade data and determine whether resulting parameter estimates are consistent with those obtained with raw data. (Foote 2001, Table. 2)

2. **Robustness**: Simulate data *while violating assumptions of the model*; check whether parameters can be recovered despite violation of assumptions. (Foote 2001, Figs. 10,11)

3. **Consistency with other data**: Do parameters estimated with model agree with those estimated independently from other data sources? (Foote 2001, Figs. 5,6; Foote 2003, Fig. 5)

**C. Application to Phanerozoic marine animal genera from Sepkoski (2002)**: principal results

1. For most peaks in observed rates there is a corresponding peak in “true” rates, but the observed and “true” peaks need not coincide temporally.
2. Estimated “true” rates are more volatile; observed rates show Signor-Lipps effect (smearing) even at stage level.

3. Estimated $p$ and $q$ similar whether $r$ assumed constant or fully time-varying. This suggests that effects of general incompleteness (smearing) are more important than effects of variation in sampling.

4. Extinction record has higher fidelity than origination record.

D. Selection among alternative models of varying complexity

1. General approach
   a. For each model, calculate the AIC = $-2S + 2k$, where $S$ is the support corresponding to the maximum likelihood solution, and $k$ is the number of parameters.
   b. Select the model with the lowest AIC. If a more complex model has higher $S$ but also higher AIC, then the increase in support is not considered sufficient to justify the added parameters. (Of course, if the two models have the same number of parameters, then the difference in AIC is just twice the difference in support.)
   c. CAVEAT: AIC is an approximation that holds best for very large sample sizes.
      • It is possible, especially with small sample sizes, to overfit, i.e. to select a more complex model using the AIC even when the data in fact resulted from a simpler model.
      • Several corrections to AIC have been proposed to deal with this (see, e.g., Connolly and Miller, 2001, *Paleobiology* 27:751-767).
      • Another approach is to simulate data with the simpler model, fit with both the simple and complex model, and check whether the more complex model is being (inappropriately) preferred (see, e.g., Foote, 2005, *Paleobiology* 31:6-20).

   a. Estimating $(\vec{p}, \vec{q}, \vec{r})$ with constant versus time-varying turnover (among intervals): variable turnover preferred
   b. Estimating $(\vec{p}, \vec{q}, \vec{r})$ with constant versus time-varying sampling (among intervals): variable sampling preferred
   c. Comparing fit of data on first and last appearances to constant vs. pulsed turnover models
      • With pulsed model, taxa extend all the way through interval of first and last appearance. They therefore have a better chance of being sampled in these intervals.
      • Stronger support for pulsed turnover, especially with respect to extinction.
      • NB: Distinction between pulsed and continuous turnover models is possible because empirical sampling rates are within the range of values for which the two models make substantially different predictions.