Lab 11: Fixed and Random Effects Life-table Response Experiments (LTRE)

Objectives: In the exercises we have completed so far, we have been estimating matrix properties for single matrices. Sometimes multiple matrices are available for different ecological conditions: multiple years, different geographic areas, or experimental treatments (e.g., burned vs. unburned). The methods of Life-table Response Experiments can be used to decompose the differences population growth rate among matrices ($\Delta\lambda$), and to determine which demographic rates are making the greatest contributions. Both fixed effects and random effects models are possible, and can be applied to either matrix elements or to the lower-level demographic rates.

Theory

The formula for calculating demographic contributions of matrix elements in a fixed effect LTRE analysis is given by:

$$\Delta\lambda = \lambda^m - \lambda^r \approx \sum_{i,j} (a_{ij}^m - a_{ij}^r) \left.\frac{\partial\lambda}{\partial a_{ij}}\right|_{A^+} \quad \text{where } A^+ = \frac{(A^m + A^r)}{2}$$

This formula states that the difference in population growth rates (λ) between a manipulated (*m*) and a reference matrix (*r*) is approximated by the sum of: the differences between the matrix cells of the manipulated and reference matrices ($a_{ij}^m - a_{ij}^r$) and the sensitivity values of the matrix cells estimated for a matrix that is the average of the elements of the two matrices (A^m and A^r).

The formula for calculating demographic contributions of lower-level demographic rates in a fixed effect LTRE analysis is given by:

$$\Delta\lambda = \lambda^m - \lambda^r \approx \sum_{i,j} (x_{ij}^m - x_{ij}^r) \left.\frac{\partial\lambda}{\partial x_{ij}}\right|_{A^+} = \sum_{i,j} (x_{ij}^m - x_{ij}^r) \left.\frac{\partial\lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}\right|_{A^+}$$

This formula states that the difference in population growth rates (λ) is approximated by the sum of: the differences between the demographic rates of the manipulated and reference matrices ($a_{ij}^m - a_{ij}^r$) and the lower level sensitivity values for a matrix that is the average of the demographic rates for the two matrices.

The formula for calculating demographic contributions of matrix elements in a random effects LTRE analysis is given by:

$$\mathrm{Var}(\lambda) \approx \sum_{i,j} \sum_{k,l} \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial\lambda}{\partial a_{kl}} \mathrm{Cov}(a_{ij}, a_{kl})$$

Here, the first two terms are sensitivity values for a mean matrix of all the matrices in the sample set. The last term is a variance covariance matrix for all of the cells in the model, where the diagonal elements are the variances and the off-diagonal elements are the covariances between pairs of matrix elements.

Example 1: Fixed effects LTRE for a savannah grass

In the first example, we will consider LTRE analyses for matrix elements for the savannah grass *Andropogon semiberbis* from a field study in Venezuela (Silva et al. 1991). This grass has four stages: 1 = 1 tiller, 2 = 2-10 tillers, 3 = 11-20 tillers and 4 = > 20 tillers. The fecundity, survival and growth rates of all four stage-classes differ under burned and unburned conditions:

$$A^{\text{burn}} = \begin{pmatrix} 0.08 & 1.63 & 2.42 & 4.40 \\ 0.21 & 0.64 & 0.35 & 0.16 \\ 0 & 0.19 & 0.43 & 0.24 \\ 0 & 0.03 & 0.23 & 0.48 \end{pmatrix} \text{ and } A^{\text{unburn}} = \begin{pmatrix} 0 & 0.71 & 0.39 & 3.59 \\ 0.018 & 0.16 & 0.14 & 0.09 \\ 0 & 0.08 & 0.07 & 0.21 \\ 0 & 0 & 0.01 & 0.07 \end{pmatrix}$$

with the result that the population growth rates differ between the matrices for the two treatments: $\lambda^{\text{burn}} = 1.2524$ and $\lambda^{\text{unburn}} = 0.2762$. The question then becomes: which of the matrix element(s) are driving the difference in population growth rates?

Calculations in Matlab

All of the necessary calculations for LTRE analyses can be conducted in Program Matlab. The first step is to create a new m-file named `grass`. The first lines of code needed are to import the two matrices. Type the following:

```
matb = [0.08 1.63 2.42 4.40; 0.21 0.64 0.35 0.16; 0 0.19 0.43
0.24; 0 0.03 0.23 0.48]
matu = [0 0.71 0.39 3.59; 0.018 0.16 0.14 0.09; 0 0.08 0.07
0.21; 0 0 0.01 0.07]
```

The next two steps are to calculate the matrix of differences and the matrix of sensitivity values for the mean matrix A^+. To calculate a matrix of differences, it is necessary to arbitrarily select one matrix to be a reference matrix. Since the unburned matrix has consistently lower demographic rates, it can be the reference matrix and all contributions will be positive values. Recall that addition and subtraction are done on an element by element basis for matrices. Type the following.

```
matdiff = matb - matu
mat = (matb + matu) / 2
```

To obtain the sensitivity values for the mean matrix (`mat` or A^+), you will need to cut and paste all of the code for those calculations from the m-file you developed for the killer whale. Once you have the sensitivity values, it should be easy to calculate a matrix of contribution values. The sum of the values in the matrix of contributions should be identical to the difference in population growth rates between the burned and unburned matrices.

```
c = matdiff .* sens
difflamb = sum(sum(c))
```

Examine the matrix of contribution values. Which demographic rates and which tiller stage-classes are having the greatest effect on the difference in population growth rates?

Example 2 Random effects LTRE for killer whales

Brault and Caswell (1993) present a stage-classified projection matrix for killer whales:

$$A = \begin{pmatrix} 0 & F_2 & F_3 & 0 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

In the Appendix of their paper, estimates for these eight matrix elements are presented for 18 different pods, 3 in southern B.C. and 15 in northern B.C. These matrices can be downloaded from the class website as `killerapp.m`

```
J01=[0 0.0067 0.1632 0; 0.9535 0.8827 0 0; 0 0.0802 0.9586 0; 0
0 0.0414 0.9752];
K01=[0 0.0062 0.1737 0; 1.0000 0.9020 0 0; 0 0.0694 0.9582 0; 0
0 0.0418 0.9855];
L01=[0 0.0037 0.0988 0; 0.9562 0.9030 0 0; 0 0.0722 0.9530 0; 0
0 0.0406 0.9798];
A01=[0 0.0043 0.1148 0; 1.0000 0.9015 0 0; 0 0.0727 0.9515 0; 0
0 0.0485 0.9667];
A04=[0 0.0042 0.1054 0; 0.8165 0.8903 0 0; 0 0.0774 0.9515 0; 0
0 0.0485 0.9810];
A05=[0 0.0027 0.0732 0; 1.0000 0.9123 0 0; 0 0.0730 0.9515 0; 0
0 0.0485 0.9545];
B01=[0 0.0025 0.0651 0; 1.0000 0.9254 0 0; 0 0.0746 0.9515 0; 0
0 0.0485 0.9810];
C01=[0 0.0047 0.1159 0; 1.0000 0.9200 0 0; 0 0.0800 0.9706 0; 0
0 0.0294 0.9608];
D01=[0 0.0068 0.1761 0; 1.0000 0.9241 0 0; 0 0.0759 0.9562 0; 0
0 0.0438 1.0000];
G01=[0 0.0061 0.1418 0; 1.0000 0.9167 0 0; 0 0.0833 0.9286 0; 0
0 0.0714 1.0000];
G12=[0 0.0050 0.1251 0; 1.0000 0.9216 0 0; 0 0.0784 0.9515 0; 0
0 0.0485 0.9810];
H01=[0 0.0021 0.0542 0; 1.0000 0.9254 0 0; 0 0.0746 0.9515 0; 0
0 0.0485 0.9810];
I01=[0 0.0027 0.0732 0; 1.0000 0.9286 0 0; 0 0.0714 0.9515 0; 0
0 0.0485 0.9810];
I02=[0 0.0045 0.1220 0; 1.0000 0.9286 0 0; 0 0.0714 0.9515 0; 0
0 0.0485 1.0000];
I11=[0 0.0052 0.1428 0; 1.0000 0.9286 0 0; 0 0.0714 0.9515 0; 0
0 0.0485 0.9810];
I18=[0 0.0037 0.0998 0; 1.0000 0.9286 0 0; 0 0.0714 0.9515 0; 0
0 0.0485 0.9810];
I31=[0 0.0047 0.1273 0; 1.0000 0.9286 0 0; 0 0.0714 0.9515 0; 0
0 0.0485 0.9810];
R01=[0 0.0024 0.0797 0; 1.0000 0.8929 0 0; 0 0.0595 0.9515 0; 0
0 0.0485 1.0000];
```

Ordinarily, the first step would be to calculate a mean matrix for all of these 18 matrices and then calculate the sensitivity values for the overall mean matrix. This step has already been conducted and is appended to the bottom of `killerapp.m` as follows:

```
% Sensitivity matrix;
S = [0.0422 0.3608 0.3686 0.3699;
     0.0443 0.3785 0.3867 0.3881;
     0.0663 0.5670 0.5793 0.5813;
     0      0      0      0     ];
```

The trickiest part of the calculations is calculating the variance-covariance matrix for all of the 18 matrices. The first step is to load all of the 18 matrices into one master matrix so that each pod becomes a separate column. To complete this step, type the following:

```
matrices=[J01(:) K01(:) L01(:) A01(:) A04(:) ...
A05(:) B01(:) C01(:) D01(:) G01(:) G12(:) ...
H01(:) I01(:) I02(:) I11(:) I18(:) I31(:) R01(:)]
```

The three trailing dots tell Matlab that the line of code continues on a second line. Only one line of Matlab code is needed to calculate the variance-covariance matrix for all of these 18 matrices. The original matrix is 4 x 4, thus the variance-covariance matrix will be 16 x 16. Elements on the diagonal are the variances of the matrix elements, and the offdiagonal elements are the covariances. Type the following:

```
covmat=cov(matrices')
```

The final step is to calculate the contributions of the demographic rates by multiplying the variance-covariance matrix by the sensitivity matrix. Here, the sensitivity matrix is also converted to a vector. In the middle term it is a vertical vector with 16 rows and 1 column, and in the last term of the equation the vector is transposed to be 1 row with 16 columns. Type the following:

```
contmat=covmat.*(S(:)*S(:)');
```

To calculate the matrix of contribution values, it is necessary to conduct some summary steps. First, the contribution values are summed across columns and then scaled to sum to one. The resulting vector is then put back into the same format as the original matrix. These then are the contribution values for each of the matrix cells for a random design LTRE analyis.

```
c = (sum(contmat))'
c = c/sum(c);
contrib=[c(1:4) c(5:8) c(9:12) c(13:16)]
```

Program Matlab has the capability of plotting matrix values in a graphical format. The following code will generate the same plot as seen in Fig. 3 of Brault and Caswell (1993). The only difference is that the plots are not rotated to the same orientation.

```
subplot(1,2,1);
  surf(covmat)
    view(52.5,30)
    axis([0 17 0 17 -0.001 .002])
subplot(1,2,2);
  surf(contmat)
    view(52.5,30)
    axis([0 17 0 17 -0.0001 0.0002])
```