Demographic heterogeneity

Introduction

Last year, Brett Melbourne and Alan Hastings [1] pointed out that there's another source of stochasticity to consider: demographic heterogeneity. Demographic stochasticity arises because individuals with the same probability of survival and the same expected fecundity may or may not survive and may have different numbers of offspring.

But there are also obviously differences among individuals in how likely they are to survive and in how many offspring they can expect to produce. Those differences reflect demographic heterogeneity. I know that most or all of you aren't as enamored of mathematical equations as I am, but stick with me for a minute here. I think this mathematical digression will help you to see what's going on.

A stochastic Ricker model

Let's start at time t with a population having N_t females. Assume that the ith female produces $B_{i,t}$ offspring, where $B_{i,t}$ is a Poisson random variable with mean and variance $\beta_{i,t}$.[1] Demographic stochasticity is reflected in the fact that the *actual* number of offspring the ith female produces is a random variable, i.e., we don't know it with certainty. We can only specify its mean and variance. Demographic heterogeneity is reflected in the fact that I have a subscript i on $\beta_{i,t}$, meaning that the expected number of offspring produced may differ from female to female. We'll assume that $\beta_{i,t}$ is drawn from a gamma distribution with mean β_t and shape parameter k_D.[2] The fact that I also have a subscript t on $\beta_{i,t}$ should clue you in to the fact that I'm going to let β_t vary over time. That's environmental stochasticity. We'll assume that β_t is drawn from a gamma distribution with mean β and shape parameter k_E.

[1] If you don't know what a Poisson random variable is, all you really need to know is that it's a reasonable choice, and that it has the property that its mean and variance are equal to one another.

[2] If you don't know what a gamma distribution is, don't worry. All you need to know is that it's a handy distribution, and that the shape parameter is related to the variance. The smaller the shape parameter, the larger the variance.

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Stochasticity	R	α	k_D	k_E	L	ΔAIC
None	2.526	0.003636	-	-	-406.5	336
Demographic	2.638	0.003744	0.01463	-	-246.3	18
Environmental	2.706	0.003800	-	1.9913	-265.3	148
Demographic & sex	2.621	0.003731	0.3876	-	-245.8	17
Environmental & sex	2.770	0.003831	-	13.1014	-242.6	10
All	2.613	0.003731	1.1475	26.6221	-236.4	

Table 1: Parameter estimates for different models fit to an experimental population of *Tribolim castaneum* [1]. $R = \beta(1-m)$. L is the log likelihood at its maximum. ΔAIC is a measure of how much worse each model is than the one below it. Differences of 10 or more are regarded as very substantial.

Now suppose that each offspring (irrespective of whether it's male or female) survives to adulthood with probability se^{-aN_t}, i.e., that there's demographic stochasticity in survival, but no demographic heterogeneity and no sex-specific survival. We will also suppose that each surviving offspring is female with probability z, i.e., that there's demographic stochasticity associated with sex determination.

An application

This model may seem complicated, but it's still relatively simple. For example, we don't allow generations to overlap, and we assume that sexes survive with the same probability and that there's no individual heterogeneity in probability of survival. Still it's complicated enough to capture what seem to be the most important features of population dynamics in one simple experimental system: laboratory populations of the flour beetle, *Tribolium castaneum*.

The results in Table 1 clearly show that all sources of stochasticity contribute importantly to population dynamics in this experimental population. Interestingly, the variance associated with demographic heterogeneity is substantially greater than the variance associated with environmental stochasticity, i.e., differences among individuals *within* a generation matter more than differences *among* generations.

References

[1] Brett A. Melbourne and Alan Hastings. Extinction risk depends strongly on factors contributing to stochasticity. *Nature*, 454(7200):100–103, 2008. 10.1038/nature06922.

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